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1984

VOLUME I
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8401

Pleuronectiformes: Development

E. H. Ahlstrom, K. Amaoka, D. A. Hensley,
H. G. Moser and B. Y. Sumida

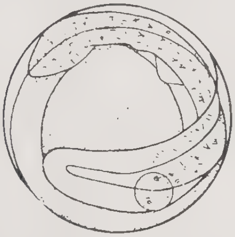
PLEURONECTIFORM fishes have both eyes on one side of the head in juveniles and adults. The eyes are symmetrical in larvae, and migration of either the left or right eye occurs during metamorphosis. In some flatfish groups the eyes are on the left side (sinistral) while in others they are on the right side (dextral); relatively few species are indiscriminate. In some flatfishes the ocular nerve of the migrating eye usually lies dorsal to the other nerve in the optic chiasma; in other groups the nerve of the migrating eye is dorsal or ventral in the chiasma with about equal frequency. In most groups the nasal organ of the blind side also migrates to a position near the dorsal midline. Features of the dentition and cranial osteology may also show asymmetry. Flatfishes are highly compressed with the underside of the body usually unpigmented. The lateral line may be lacking on the blind side; the pectoral fin is often shorter on the blind side and has fewer rays; the pelvic fin on the blind side is often shorter, smaller and differently placed with respect to the ventral midline compared with the pelvic fin on the ocular side; squamation may be different on the two sides of the body. The dorsal and anal fins are long-based; the dorsal extends anteriad to at least the eye in all flatfishes except *Psettodes* and the anal fin extends well forward of the first haemal spine. The caudal fin is typically rounded or truncate with few or no secondary rays. Pleuronectiforms are benthic carnivores, occurring worldwide, primarily in shallow to moderate depths, with some representatives in brackish and fresh water habitats. Nelson (1976) notes a total of 520 species.

The classification presented below is based on the works of Regan (1910, 1929) and Norman (1934, 1966) with modifications by Hubbs (1945), Amaoka (1969), Hensley (1977), and Futch (1977). Our removal of *Perissias* from the Paralichthyidae and placement in the Bothidae are based on previously unpublished information. Those genera marked with an asterisk are misplaced in this classification and are discussed in this paper and in Hensley and Ahlstrom (this volume).

- Order Pleuronectiformes
  - Suborder Psettodoidei
    - Family Psettodidae (Indo-Pacific, West Africa)
      - *Psettodes*
  - Suborder Pleuronectoidei
    - Family Citharidae
      - Subfamily Brachypleurinae (Indo-Pacific)
        - *Brachypleura,* Lepidoblepharon*
      - Subfamily Citharinae (Indo-Pacific, Mediterranean, West Africa)
        - *Citharoides, Eucitharus*
    - Family Scophthalmidae (North Atlantic, Mediterranean, Black Sea)
      - *Lepidorhombus, Phrynorhombus, Scophthalmus, Zeugopterus*
    - Family Paralichthyidae (Western and Eastern Atlantic, Eastern Pacific, Indo-Pacific)
      - *Ancylopsetta, Cephalopsetta, Citharichthys, Cyclop-*

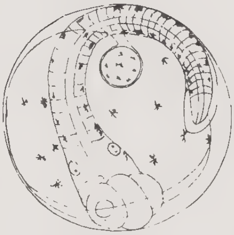
Fig. 341. Eggs of Pleuronectiformes. Captions in each illustration indicate the species and diameter of the egg in mm. *Scophthalmus maeoticus maeoticus,* from Dekhnik, 1973; *Paralichthys olivaceus,* from Mito, 1963; Bothidae, from Mito, 1963; *Limanda aspera,* from Pertseva-Ostroumova, 1954; *Hippoglossoides dubius,* from Pertseva-Ostroumova, 1961; *Microstomus pacificus,* original, CalCOFI; *Pleuronichthys cornutus,* from Mito, 1963; *Pelotretis flavilatus,* from Robertson, 1975a; *Peltorhamphus novaezeelandiae,* from Robertson, 1975a; *Trinectes maculatus,* from Hildebrand and Cable, 1938; *Pegusa lascaris nasuta,* from Dekhnik, 1973; *Cynoglossus robustus,* from Fujita and Uchida, 1957.

1.10 - 1.33



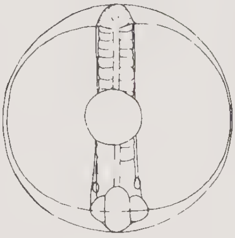
Scophthalmus maeoticus maeoticus

0.92



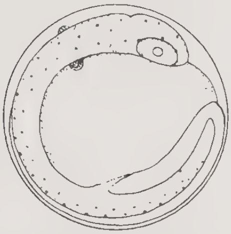
Paralichthys olivaceus

0.64



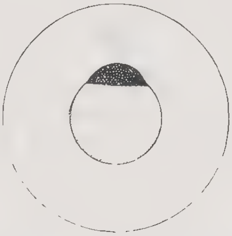
Bothidae

0.76 - 0.85



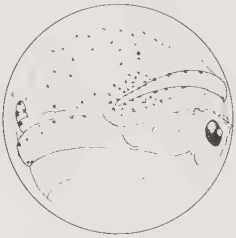
Limanda aspera

2.10 - 2.94



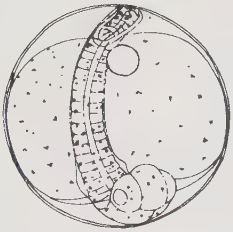
Hippoglossoides dubius

2.05 - 2.57



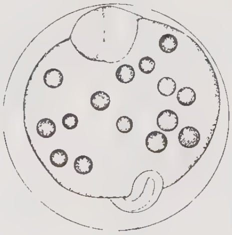
Microstomus pacificus

1.22



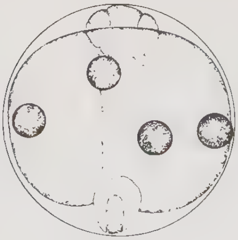
Pleuronichthys cornutus

0.62 - 0.68



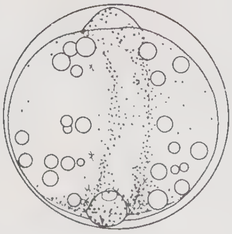
Pelotretis flavilatus

0.62 - 0.68



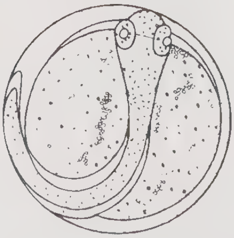
Peltorhamphus novaezeelandiae

0.67 - 0.86



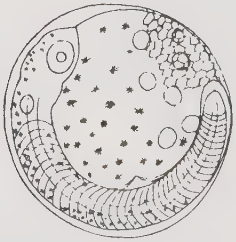
Trinectes maculatus

1.09 - 1.35



Pegusa lascaris nasuta

0.85 - 0.90



Cynoglossus robustus

TABLE 170. CHARACTERS OF EGGS OF PLEURONECTINAE SPECIES WHICH LACK OIL GLOBULES.

Species	Region[1]	Type of egg (pelagic or demersal)	Egg size (mm)	Chorion	References
Cleisthenes herzensteini	WNP	P	0.84–1.03	—	Pertseva-Ostroumova, 1961
Embassichthys bathybius	ENP	P	3.0	smooth	Richardson, 1981b
Eopsetta grigorjewi	WNP	P	1.10–1.20	striations	Yusa, 1961; Fujita, 1965
E. jordani	ENP	P	1.21–1.25	smooth	Alderdice and Forrester, 1971
Glyptocephalus cynoglossus	NA	P	1.07–1.25	striations	Cunningham, 1887; Ehrenbaum, 1905–1909
G. stelleri	WNP	P	1.20–1.61	thick, reticulate	Pertseva-Ostroumova, 1961; Dekhnik, 1959
G. zachirus	ENP	P	1.9–2.15	striations	Original
Hippoglossoides dubius	WNP	P	2.10–2.94	smooth	Pertseva-Ostroumova, 1961
H. elassodon	NP	P	2.45–3.75	smooth	Thompson and Van Cleve, 1936; Pertseva-Ostroumova, 1961
H. platessoides	WNA	P	1.38–2.64	smooth	Russell, 1976 (summary)
H. robustus	WNP	P	2.04–2.69	smooth, thin	Pertseva-Ostroumova, 1961
Hippoglossus hippoglossus	NA	P	3.0–3.8	smooth, thick	Tåning, 1936; Pertseva-Ostroumova, 1961
H. stenolepis	NP	P	2.9–3.8	minute honeycomb structure	Thompson and Van Cleve, 1936
Isopsetta isolepis	ENP	P	0.90–1.10	smooth	Richardson et al., 1980
Kareius bicoloratus	WNP	P	1.00–1.15	reticulate	Pertseva-Ostroumova, 1961
Lepidopsetta bilineata	NP	D	1.02–1.09	sticky-orange	Pertseva-Ostroumova, 1961
L. mochigarei	WNP	D	0.87–0.95	thick, gluey	Pertseva-Ostroumova, 1961
Limanda aspera	NP	P	0.76–0.85	smooth	Pertseva-Ostroumova, 1954
L. ferruginea	WNA	P	0.79–1.01	striations	Miller, 1958; Colton and Marak, 1969
L. limanda	ENA	P	0.66–1.20	—	Russell, 1976 (summary)
L. punctatissima	WNP	P	0.66–0.87	smooth	Pertseva-Ostroumova, 1961
L. proboscidea	WNP	P	0.72–0.87	smooth	Pertseva-Ostroumova, 1961
L. schrenki	WNP	D	0.73–0.83	adhesive	Yusa, 1960a
L. schrenki (as *Pseudopleuronectes yokohamae*)	WNP	D	0.74–0.83	adhesive	Pertseva-Ostroumova, 1961
L. yokohamae	WNP	D	0.81–0.84	adhesive	Yusa, 1960a, b
Liopsetta glacialis	NP	P	1.20–1.60	thin	Pertseva-Ostroumova, 1961
L. obscura	WNP	D	0.78–0.94	thick, sticky	Pertseva-Ostroumova, 1961
L. pinnifasciata	WNP	P	1.43–1.66	thin, folds	Pertseva-Ostroumova, 1961
Lyopsetta exilis	ENP	P	1.47–1.68	smooth	Original; Ahlstrom and Moser, 1975
Microstomus kitt	WNA	P	1.13–1.45	striations	Russell, 1976; Dekhnik, 1959
M. pacificus	ENP	P	2.05–2.57	smooth	Original; Ahlstrom and Moser, 1975
Parophrys vetulus	ENP	P	0.89–0.93	striations	Budd, 1940; Original
Platichthys flesus	ENA	P	0.80–1.13	—	Russell, 1976 (summary)
P. f. luscus	B	P	1.05–1.35	smooth	Dekhnik, 1973
P. stellatus	NP	P	0.89–1.01	smooth, thin	Orcutt, 1950; Yusa, 1957
Pleuronectes pallasii	NP	P	1.67–2.21	—	Pertseva-Ostroumova, 1961
P. platessa	ENA	P	1.66–2.17	—	Russell, 1976 (summary)
Pleuronichthys coenosus	ENP	P	1.20–1.56	polygonal pattern	Sumida et al., 1979; Budd, 1940
P. decurrens	ENP	P	1.84–2.08	polygonal pattern	Sumida et al., 1979; Budd, 1940
P. verticalis	ENP	P	1.00–1.16	polygonal pattern	Sumida et al., 1979; Budd, 1940
Psettichthys melanostictus	ENP	P	ca. 1.0	—	Hickman, 1959
Pseudopleuronectes americanus	WNA	D	0.71–0.96	adhesive	Breder, 1923
P. herzensteini	WNP	P	0.80–1.0	smooth	Pertseva-Ostroumova, 1961
Reinhardtius hippoglossoides	NA/NP	P	4.00–4.50	—	Jensen, 1935
Tanakius kitaharai	WNP	P	1.20–1.30	striations	Fujita, 1965
Verasper variegatus	WNP	P	1.60–1.64	smooth	Takita et al., 1967; Mito, 1963

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[1] B = Black Sea. ENA = eastern North Atlantic. ENP = eastern North Pacific. I = India. NA = North Atlantic. NP = North Pacific. WNA = western North Atlantic. WNP = western North Pacific.

setta, Etropus, Gastropsetta, Hippoglossina, Lioglossina, Paralichthys, Pseudorhombus, Syacium, Tarphops, Tephrinectes, Thysanopsetta,* Verecundum, Xystreurys*

Family Bothidae

Subfamily Taeniopsettinae (Western Atlantic, Eastern Pacific, Indo-Pacific)

Engyophrys, Perissias, Taeniopsetta, Trichopsetta

Subfamily Bothinae (Indian, Pacific, Atlantic, Mediterranean, Southern oceans)

Arnoglossus, Asterorhombus, Bothus, Chascanopsetta, Crossorhombus, Engyprosopon, Grammatobothus, Japonolaeops, Kamoharaia, Laeops, Lophonectes, Monolene, Mancopsetta, Neo-*

TABLE 171. CHARACTERS OF PLEURONECTIFORM EGGS WITH A SINGLE OIL GLOBULE.

Taxon	Region[1]	Egg size (mm)	Oil globule size (mm)	Chorion	Size at hatching (mm)	References
Pleuronectidae						
Hypsopsetta guttulata	ENP	0.78–0.89	0.12–0.14	smooth	1.7–2.3	Sumida et al., 1979; Eldridge, 1975
Pleuronichthys cornutus	WNP	1.03–1.25		polygonal pattern	2.8–3.8	Mito, 1963; Takita and Fujita, 1964
P. ritteri	ENP	0.94–1.08	0.08–0.14	polygonal pattern	2.1	Sumida et al., 1979
Scophthalmidae						
Lepidorhombus whiffiagonis	ENA	1.02–1.22	0.25–0.30	striations	ca. 4.0	McIntosh, 1892; Holt, 1893
Phrynorhombus norvegicus	ENA	0.72–0.92	0.09–0.16	rugose	2.5–2.8	Ehrenbaum, 1905–1909; Hefford, 1910
P. regius	ENA	0.90–0.99	0.16–0.18	—	2.4	Holt, 1897
Scophthalmus aquosus	WNA	0.90–1.38	0.15–0.30	striations	ca. 2.0	Martin and Drewry, 1978 (summary)
S. maeoticus	B	1.10–1.33	0.17–0.23	—	3.5 TL	Dekhnik, 1973
S. maximus	ENA	0.90–1.20	0.15–0.22	rugose	2.1–3.0	Holt, 1892; Jones, 1972
S. rhombus	B	1.20–1.50	0.16–0.25	striations	3.8	Jones, 1972
Zeugopterus punctatus	ENA	0.92–1.07	0.17–0.20	—	2.5–2.9	Hefford, 1910
Paralichthyidae						
Hippoglossina oblonga	WNA	0.91–1.12	0.17	smooth	2.7–3.2	Miller and Marak, 1962
H. stomata	ENP	1.22–1.38	0.20–0.26	smooth	3.7	Sumida et al., 1979
Paralichthys californicus	ENP	0.74–0.82	0.10–0.19	smooth	ca. 2.0	Original
P. dentatus	WNA	0.90–1.10	0.18–0.31	—	2.4–2.8	Smith and Fahay, 1970
P. olivaceus	WNP	0.83–1.03	0.13–0.21	smooth	2.6–2.8	Mito, 1963
Pseudorhombus cinnamoneus	WNP	0.77–0.89	0.12–0.14	—	1.8–2.0	Mito, 1963
Citharichthys arctifrons	WNA	0.70–0.82	—	smooth	ca. 2.0	Richardson and Joseph, 1973
Bothidae						
Arnoglossus capensis	ESA	0.72	0.12	smooth	2.2	Brownell, 1979
A. kessleri	B	0.59–0.70	0.10–0.13	smooth	1.8–1.9	Dekhnik, 1973
A. laterna	ENA	0.60–0.76	0.11–0.15	smooth	2.6	Russell, 1976 (summary)
A. scapha	NZ	0.78–0.88	0.11–0.12	smooth	—	Robertson, 1975a
A. thori	ENA	0.67–0.74	0.12	smooth	1.6–2.0	Russell, 1976 (summary)

[1] ESA eastern South Atlantic, NZ = New Zealand, key to other regions as in Table 170

laeops, Parabothus, Pelecanichthys, Psettina, Tosarhombus

Family Pleuronectidae
- Subfamily Pleuronectinae (Atlantic, Mediterranean, Pacific, Arctic)
  - *Acanthopsetta, Atheresthes, Cleisthenes, Clidoderma, Dexistes, Embassichthys, Eopsetta, Glyptocephalus, Hippoglossoides, Hippoglossus, Hypsopsetta, Isopsetta, Lepidopsetta, Limanda, Liopsetta, Lyopsetta, Microstomus, Parophrys, Platichthys, Pleuronectes, Pleuronichthys, Psettichthys, Pseudopleuronectes, Reinhardtius, Tanakius, Verasper*
- Subfamily Poecilopsettinae (Indo-Pacific, Atlantic)
  - *Marleyella, Nematops, Poecilopsetta*
- Subfamily Paralichthodinae (Indian Ocean off South Africa)
  - *Paralichthodes*
- Subfamily Samarinae (Indo-Pacific)
  - *Samaris, Samariscus*
- Subfamily Rhombosoleinae (New Zealand, Southern Australia, South America)
  - *Ammotretis, Azygopus, Colistium, Oncopterus, Pelotretis, Peltorhamphus, Psammodiscus, Rhombosolea*

Suborder Soleoidei
- Family Soleidae
  - Subfamily Soleinae (Worldwide, tropical to temperate) Norman (1966) recognized 22 genera
  - Subfamily Achirinae (American coasts, some fresh water) Norman (1966) recognized 9 genera
- Family Cynoglossidae
  - Subfamily Symphurinae (Tropical-Subtropical American coasts, Mediterranean, West Africa, Indo-Pacific)
    - *Symphurus*
  - Subfamily Cynoglossinae (Indo-Pacific, Mediterranean, West Africa, Japan, some fresh water)
    - *Cynoglossus, Paraplagusia*

A profuse literature on the life history stages of flatfishes has accumulated since the early work of Cunningham (1887, 1889, 1890, 1891) who described numerous series reared from eggs collected from running ripe females. Other European workers (Holt, 1893; McIntosh and Prince, 1890; Petersen, 1904, 1905, 1906, 1909; Schmidt, 1904; Kyle, 1913) identified early life history series of additional species so that, by the time of Ehrenbaum's (1905–1909) summary, ontogenetic stages of a major portion of the eastern North Atlantic flatfish fauna were known. Padoa (1956k) summarized ontogenetic information on Medi-

TABLE 172. CHARACTERS OF PLEURONECTIFORM EGGS WITH MULTIPLE OIL GLOBULES.

	Region¹	Egg size (mm)	Number of oil globules	Yolk	Chorion	References
Achirinae						
Achirus lineatus	WNA	0.71–0.76	12–14	homogeneous	smooth, thin	Houde et al., 1970
Trinectes maculatus	WNA	0.67–0.86	15–34	homogeneous	smooth	Hildebrand and Cable, 1938
Soleinae						
Aesopia cornuta	WNP	1.45–1.60	many; scattered	homogeneous	polygonal mesh	Mito, 1963
Austroglossus microlepis	ESA	0.88	12–20	homogeneous	smooth	Brownell, 1979
Buglossidium luteum	ENA	0.64–0.94	12–21; scattered	peripheral	smooth	Holt, 1891; Hefford, 1910
Dicologoglossa cuneata	ENA	0.70–0.84	60–80; scattered	peripheral segmentation		Lagardere, 1980
Microchirus ocellatus	ENA	0.90–1.10	30–40; scattered	peripheral segmentation	smooth	Palomera and Rubies, 1977
M. variegatus	ENA	1.28–1.42	to 50+; scattered	peripheral segmentation	smooth	Cunningham, 1889
Pegusa impar	M	1.06				Padoa, 1956k
P. lascaris lascaris	ENA	1.28–1.38	to 50+	peripheral segmentation		Holt, 1891; Hefford, 1910
P. lascaris nasuta	B	1.36–1.38	many; clumped	homogeneous	polygonal mesh	Dekhnik, 1973
Solea solea	ENA	0.98–1.58	many; highly clumped	peripheral segmentation	smooth	Cunningham, 1889; Fabre-Domergue and Biétrix, 1905
Synaptura kleini	ESA	1.34	many; clumped	homogeneous	smooth	Brownell, 1979
Zebrias japonicus	WNP	1.75	many; scattered	homogeneous	smooth	Mito, 1963
Z. zebra	WNP	1.60	many; scattered	homogeneous		Mito, 1963
Symphurinae						
Symphurus atricauda	ENP	0.71–0.78	10–23	homogeneous	smooth, colored	Original
Cynoglossinae						
Cynoglossus capensis	ESA	0.75	2–16	homogeneous	smooth	Brownell, 1979
C. robustus	WNP	0.85–0.90	5–15	homogeneous	fine hexagonal network	Fujita and Uchida, 1957
C. (Areliscus) trigrammus	WNP	1.19–1.23	30–50	homogeneous	smooth	Fujita and Takita, 1965
Cynoglossidae no. 5	WNP	0.71	14	homogeneous	smooth	Mito, 1963
Cynoglossidae sp. A	I	0.84	13–15	homogeneous	smooth	Vijayaraghavan, 1957
Cynoglossidae sp. B	I	0.82	18–22; clustered	homogeneous	smooth	Vijayaraghavan, 1957
Cynoglossus I	I	0.60	16–30	homogeneous	smooth	Nair, 1952a
Cynoglossidae (as *Solea ovata*)	I	0.61–0.71	17–25	homogeneous	smooth	John, 1951b
Rhombosoleinae						
Ammotretis rostratus	NZ	ca. 0.8	8–11	homogeneous	smooth	Thomson, 1906
Colistium guntheri	NZ	1.0–1.08	14–26	homogeneous		Robertson, 1975a
C. nudipinnis	NZ	ca. 1.5	21–28	homogeneous		Robertson, 1975a
Pelotretis flavilatus	NZ	0.85–0.95	8–18	homogeneous	smooth	Robertson, 1975a
Peltorhamphus novaezeelandiae	NZ	0.62–0.68	2–6	homogeneous	smooth	Robertson, 1975a
P. tenuis	NZ	0.58–0.68	2–4	homogeneous	smooth	Robertson, 1975a
Rhombosolea leporina	NZ	0.58–0.70	2–7	homogeneous	smooth	Robertson, 1975a
R. plebeia	NZ	0.58–0.72	2–13	homogeneous	smooth	Robertson, 1975a; Robertson and Raj, 1971
Bothinae						
Mancopsetta maculata antarctica	S	2.45–3.00	20+	homogeneous	smooth	Efremenko et al., 1981

¹ M = Mediterranean, S = southern oceans; key to other regions as in Table 170.

terranean flatfishes and more recently Russell (1976) provided an extensive review of previous European contributions. Knowledge of ontogenetic stages of western Atlantic flatfishes is summarized by Martin and Drewry (1978) and Fahay (1983). Early life histories of North Pacific flatfishes are treated comprehensively by Pertseva-Ostroumova (1961). Japanese and Indian workers have provided a long list of contributions to flatfish life history studies and Amaoka (1969, 1979), Hensley (1977) and Futch (1977) employed ontogenetic characters in assessing phylogenetic relationships. The individual contributions to flatfish ontogeny are too numerous to summarize concisely and are cited in the section that follows.

DEVELOPMENT

Eggs

Eggs are known for most species in Pleuronectidae and Scophthalmidae and for only a few to moderate numbers of

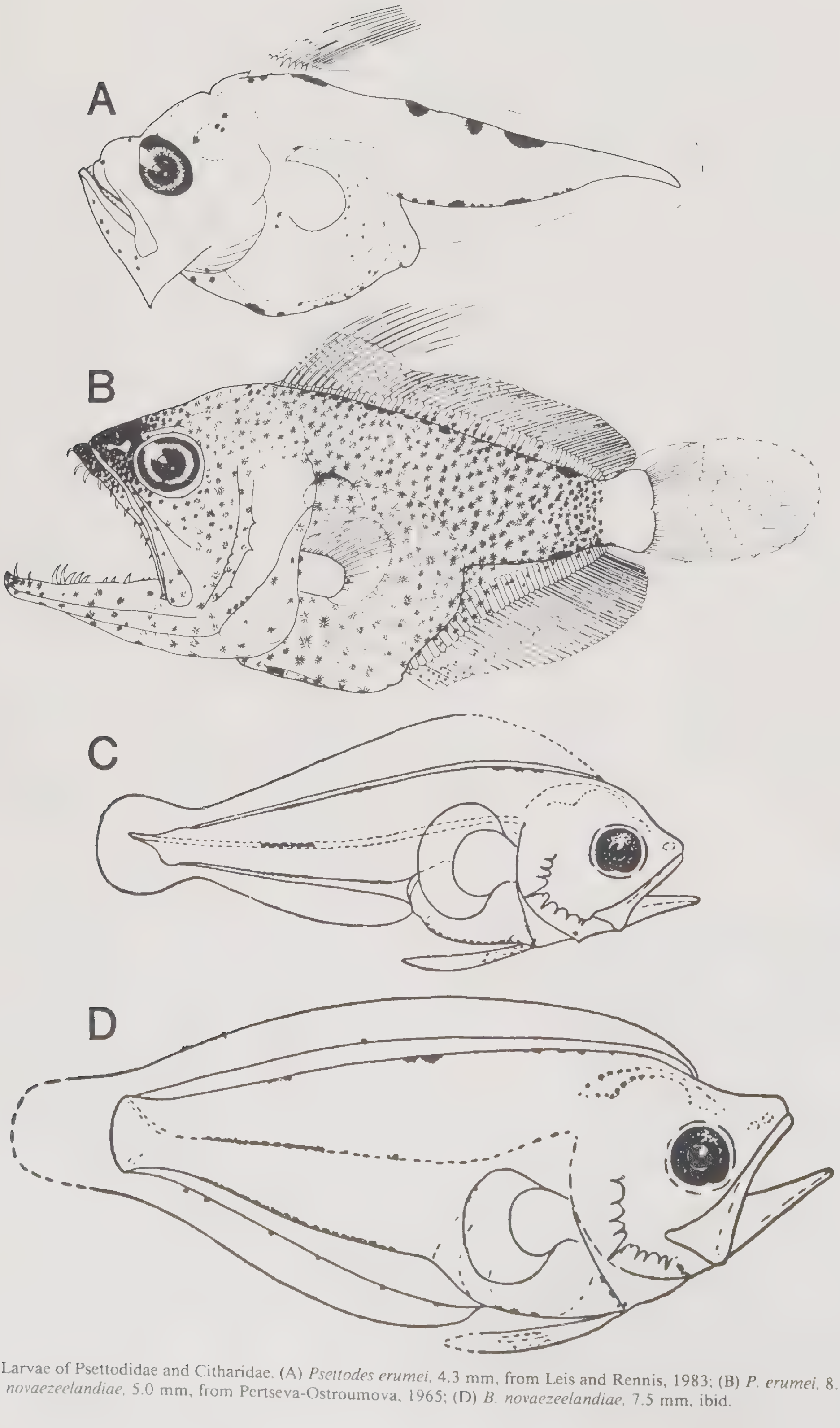

Fig. 342. Larvae of Psettodidae and Citharidae. (A) *Psettodes erumei,* 4.3 mm, from Leis and Rennis, 1983; (B) *P. erumei,* 8.7 mm, ibid; (C) *Brachypleura novaezeelandiae,* 5.0 mm, from Pertseva-Ostroumova, 1965; (D) *B. novaezeelandiae,* 7.5 mm, ibid.

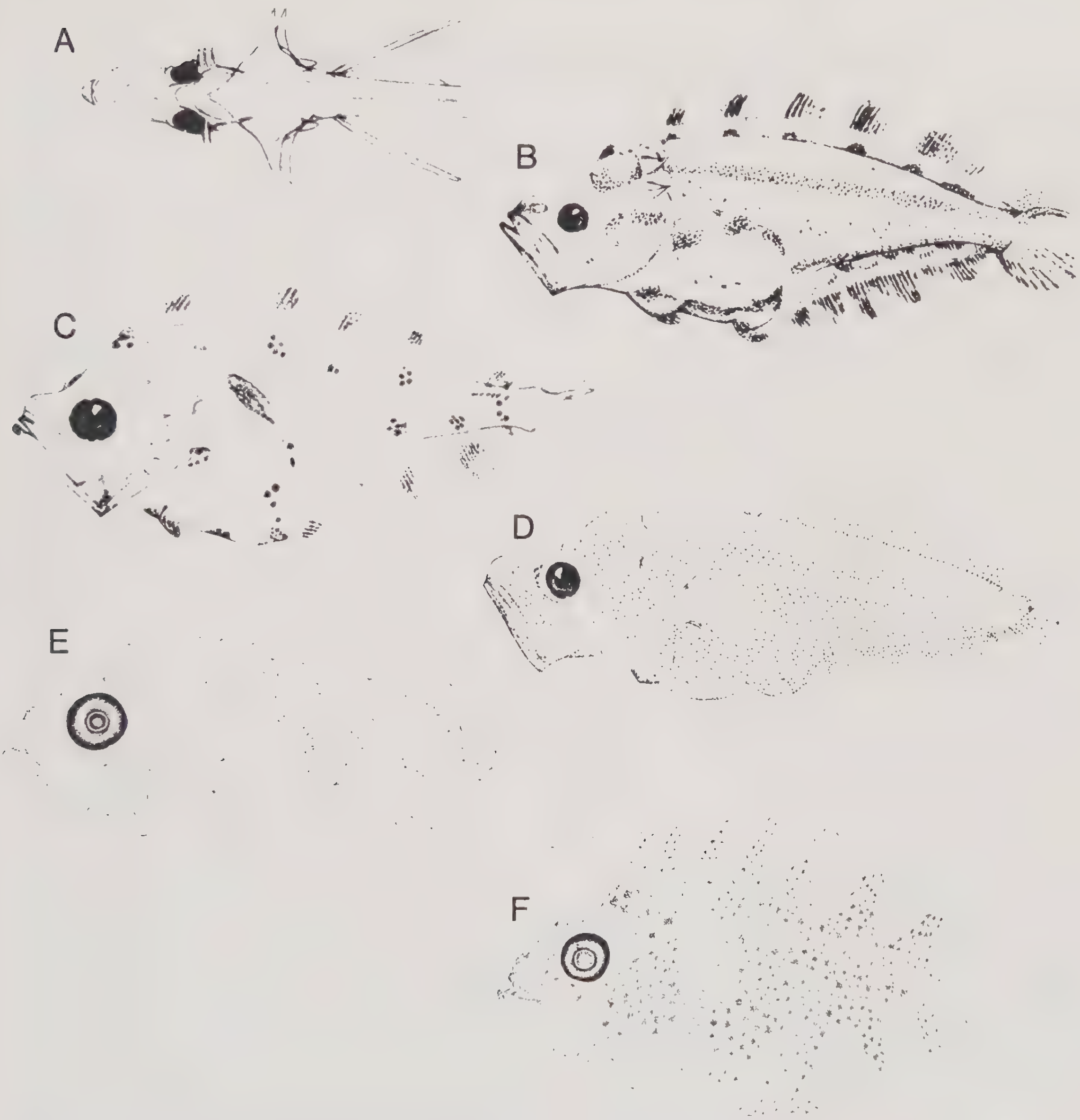

Fig. 343. Larvae of Scophthalmidae. (A) *Zeugopterus punctatus*, 8.9 mm, dorsal view, from Petersen, 1909; (B) *Z. punctatus*, 9.0 mm, ibid; (C) *Lepidorhombus boscii*, 9.7 mm, ibid; (D) *Phrynorhombus regius*, 8.0 mm, ibid; (E) *Scophthalmus maximus*, 7.4 mm, from Jones, 1972; (F) *S. rhombus*, 8.0 mm, ibid.

→

Fig. 344. Larvae of Paralichthyidae. (A) *Paralichthys californicus*, 7.0 mm, original, CalCOFI; (B) As above, dorsal view; (C) *Xystreurys liolepis*, 6.7 mm, original, CalCOFI; (D) As above, dorsal view; (E) *Hippoglossina stomata*, 8.6 mm, from Sumida et al., 1979; (F) *Pseudorhombu pentophthalmus*, 9.2 mm, from Okiyama, 1974a; (G) *Tarphops oligolepis*, 9.2 mm, ibid.

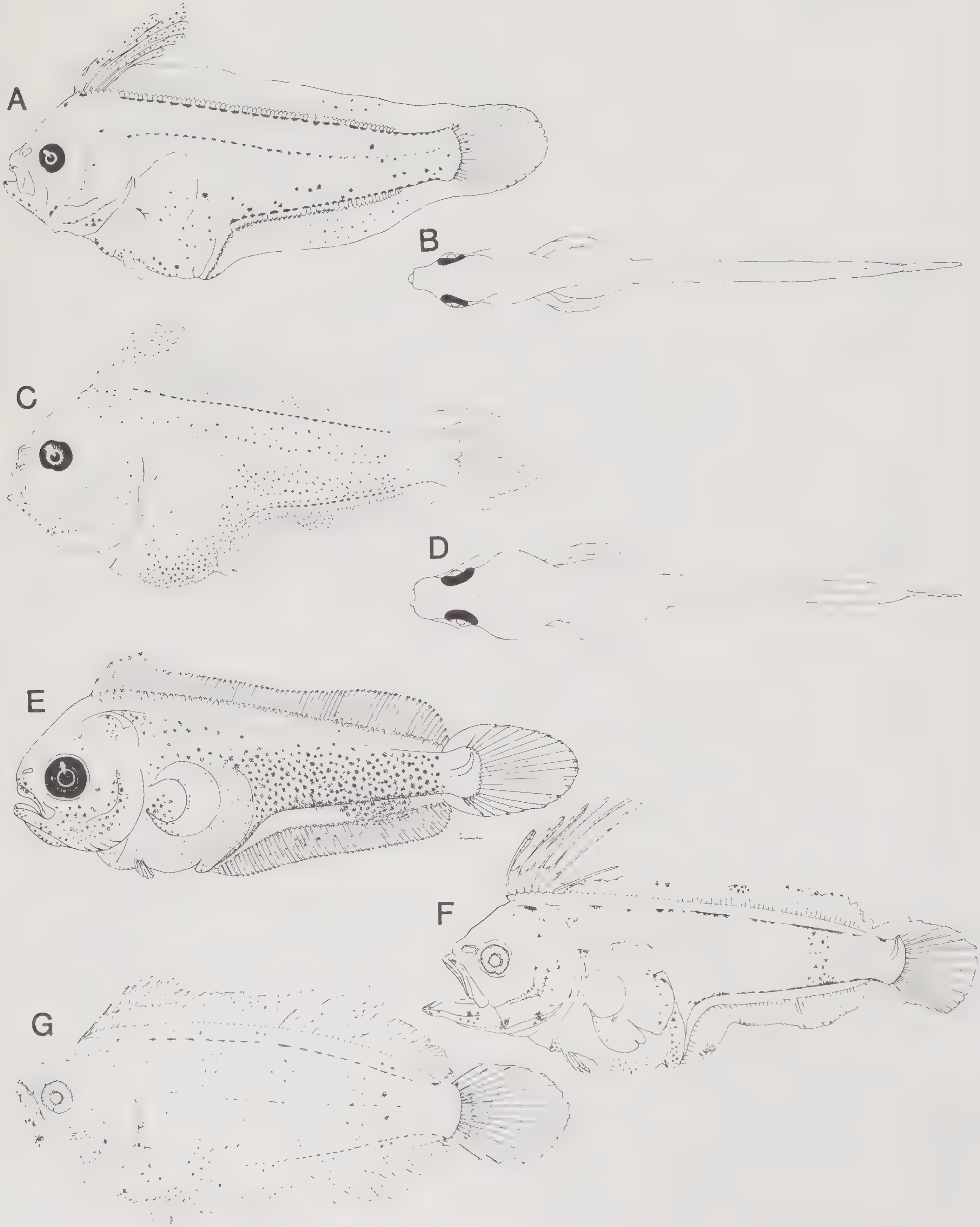
A
B
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TABLE 173. SUMMARY OF ONTOGENETIC CHARACTERS OF PLEURONECTIFORMS. (Line indicates data unavailable or presented elsewhere in column.)

	Eggs				Larvae		
Taxon	Egg size (mm)	Oil globule: Single/ Multiple/ Absent	Yolk: Homogeneous/ Segmented	Chorion: Smooth/ Striated/ Polygonal	Size at hatching (mm)	Size at metamorphosis (mm)	Elongate dorsal rays: Present (no.)/Absent
Psettodidae	—	—	—	—	—	9–10	10
Citharidae	—	—	—	—	—	—	—
Brachypleura	—	—	—	—	—	7–8	ca. 6
Scophthalmidae	0.72–1.5	S	H	St	2.0–4.0	8–>20	A
Paralichthyidae	<0.70–1.38	S	H	S	1.8–3.7	—	—
Paralichthys group	—	—	—	—	—	7.5–15	4–5
Pseudorhombus group	—	—	—	—	—	8.7–12.5	5–9
Cyclopsetta group	—	—	—	—	—	9–>35	**
Bothidae	0.59–0.88	S	H	S	1.8–2.6	—	—
Taeniopsettinae	—	—	—	—	—	19–60	1
Bothinae	—	—	—	—	—	15–120	1
Pleuronectidae	—	—	—	—	—	—	—
Pleuronectinae	0.66–4.5	A*	H	S, P, St	1.7–16.0	4.4–65	A
Poecilopsettinae	—	—	—	—	—	ca. 30	A
Samarinae	—	—	—	—	—	ca. 30	1
Rhombosoleinae	0.58–1.5	M	H	S	ca. 1.8	—	—
Soleidae	0.64–1.75	M	H, S	S, P	1.6–4.1	—	—
Soleinae	—	—	—	—	—	3.4–18	A
Achirinae	—	—	—	—	—	3–5.5	***
Cynoglossidae	0.60–1.23	M	H	S, P	1.3–3.2	—	—
Cynoglossinae	—	—	—	—	—	ca. 4–18	2
Symphurinae	—	—	—	—	—	ca. 12–32	usually 4–5

* Single oil globule present in 3 species.

** 0–2 in *Etropus*; 0, 2, 3 in *Citharichthys*; 5–8 in *Syacium*; 8–11 in *Cyclopsetta*

*** Third ray elongated in *Achirus*.

**** 0, 1, or 2 in *Citharichthys*; 2 or 3 in *Cyclopsetta* and *Syacium*; 0 or 1 in *Etropus*.

***** *S. ligulata* develops elongate third and fourth rays.

****** Protruding in *Chascanopsetta*, *Pelecanichthys*, and *Kamoharaia*.

species in other groups, including Soleidae, Cynoglossidae, Paralichthyidae, and Bothidae.

With a few exceptions, the eggs of flatfishes are pelagic, round, have homogeneous yolk, a narrow perivitelline space, and an unsculptured chorion (Fig. 341). The eggs of all flatfishes are spawned separately. The characters of eggs showing greatest differences among flatfishes are 1) egg size, and 2) the presence or absence of an oil globule(s) (Tables 170–172).

Of the approximately 60 species of pleuronectine flatfishes of the North Pacific and North Atlantic, eggs are known for at least 45 (Table 170). Six species are known to have demersal eggs; these are round or occasionally off-round and have a sticky, adhesive chorion that permits clustering or adhesion to bottom objects. Egg diameters range from 0.66 to 4.5 mm within the subfamily. The yolk is homogeneous in all pleuronectine eggs. The perivitelline space is narrow to moderate, except for eggs of *Hippoglossoides*, which have a wide perivitelline space, usually 25–30% of the egg diameter on either side of the yolk mass. The chorion has the appearance of being smooth on eggs of most species, but closer inspection reveals striations or reticulations on the chorion of some kinds. The chorion of *Pleuronichthys* eggs has a striking hexagonal pattern. The eggs of pleuronectine flatfishes, except for three species, lack an oil globule. The state of embryonic development achieved in the egg is related to egg size, more specifically to yolk size. Larvae hatching from small eggs lack eye pigment, a functional mouth and pectoral fins; those hatching from larger eggs are much more advanced, with pigmented eyes, a functional mouth and pectorals. Embryos in middle- and late-stage eggs are pigmented, with patterns varying between genera and species. Among species, yolk pigment can range from unpigmented, to some pigment on yolk adjacent to the embryo, to heavily pigmented. Pigment can also be present on finfolds of late-stage eggs of some flatfishes.

Eggs of Scophthalmidae, Paralichthyidae and Bothidae have a single, small to moderate-sized oil globule, are pelagic, round, have a narrow to moderate perivitelline space, and homogeneous yolk (Fig. 341, Table 171). In late-stage eggs and newly hatched larvae the single oil globule usually is in the rear of the yolk mass.

Eggs are known for 8 of the 10 species of scophthalmid flatfishes. They range in size from 0.72 to 1.50 mm. The chorion is striated or rugose in six species and this may apply to all. Embryos develop considerable pigment over the head and body and often in finfolds; pigment over the yolk mass and oil globule can range from none, or sparse, to intense.

Eggs are known for only a few species in the family Paralichthyidae. These range in size from 0.70–1.38 mm; chorions are unsculptured. Except for a few species of *Arnoglossus*, eggs of bothid flatfishes are practically unknown. Mito (1963) lists 10 kinds of bothid eggs off Japan, unidentified to genus; 8 of these have diameters under 1.0 mm. Eggs of his Bothidae No. 9 are slightly off-round and three different eggs have a conspicuous wart-like appendage. Much work remains to be done in identifying eggs of fishes of these families, preferably through rearing eggs from known parents.

Eggs with multiple oil globules are typical of the families

TABLE 173. EXTENDED.

Larvae								
Elongate pelvic rays: Present/Absent	Gut: Normal/Protruding/Trailing	Preopercular spines: Present/Absent	Otic region spines: Present/Absent	Frontal region spines: Present/Absent	Urohyal spines: Present/Absent	Basipterygial spines: Present/Absent	Cleithral spines: Present/Absent	Body spines: Present/Absent
A	N	P	A	A	A	A	A	A
—	—	—	—	—	—	—	—	—
P	N	P	A	A	A	A	A	A
A	N	P, A	P, A	P, A	A	A	A	A
—	—	—	—	—	—	—	—	—
A	N	P	A, P	A	A	A	A	A
A	N	P	A, P	A	A	A	A	A
****	N	P	P, A	A	A	A	A	A
—	—	—	—	—	—	—	—	—
A	N	A	P	A	P	P	P	A
A	******	A	A	A	P, A	P, A	P, A	P, A
—	—	—	—	—	—	—	—	—
A	N	A, P	A, P	A, P	A	A	A	A
A	N	A	A	A	A	A	A	A
A	P	A	A	A	A	A	A	A
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
A	N, P	A	A	A	A	A	A	A
A	N, P	A, P	A, P	A, P	A	A	A	P, A
—	—	—	—	—	—	—	—	—
A	P	A	A	A	A	A	A	A
A, *****	P, T	A	A	A	A	A	A	A

Soleidae, Cynoglossidae, the pleuronectid subfamily Rhombosoleinae, and *Mancopsetta,* previously considered a bothid (Fig. 341, Table 172). Eggs have been described for about a dozen kinds of soleids ranging in size from 0.64–1.75 mm. Eggs are round, or occasionally slightly off-round. Oil globules are usually numerous but vary in number, size and distribution within the yolk. They can be highly clumped, as in *Solea solea,* or scattered throughout the yolk, as in *Microchirus variegatus.* In eggs of the latter, oil globules were observed to range in size from 0.015–0.12 mm, whereas they are much smaller and more uniform in size in *Solea solea* or *Pegusa lascaris.* Eggs of the two achirine soleids described from the western Atlantic have a relatively low number of oil globules. Perivitelline space is narrow to negligible in soleid eggs. The yolk is peripherally segmented in eggs of the four species known from the eastern North Atlantic. Yolk is more completely segmented in the egg designated as Synapturinae No. 1 by Mito (1963). Yolk can remain unsegmented, however, as for example in *Achirus lineatus* and *Trinectes maculatus.* Although the chorion of soleid eggs is usually smooth and unsculptured, Mito (1963) found eggs of *Aesopia cornuta* to have a pattern of large hexagonal meshes, 0.18–0.24 mm wide, covering the chorion, and Dekhnik (1973) shows fine polygonal sculpturing on the chorion of *P. lascaris.*

Eggs of the few cynoglossid species known (Table 172) are small, have homogeneous yolk without secondary segmentation, a narrow perivitelline space and either an unsculptured chorion or one with small polygonal meshes. Oil globules range in number between 5–50, and can be variously distributed in the yolk.

Robertson (1975a) described eggs of seven species of Rhombosoleinae, belonging to four genera (Table 172). Egg diameters range from 0.58 to 1.5 mm. Oil globules in described eggs range in number from 2–28. Yolk is homogeneous, the perivitelline space is narrow, and the chorion is smooth.

Efremenko et al. (1981) described the ovarian and planktonic eggs of *Mancopsetta maculata antarctica* and showed that they are large (2.45–2.75 mm) and have multiple oil globules (>20). This finding provides evidence that *Mancopsetta* does not belong in the Bothidae.

Larvae

In addition to such features as meristics, fin arrangement, and osteology of the fin supports and axial skeleton (which develop gradually during ontogeny and are essential for identification of flatfish larvae) the larval stage itself provides many characters useful in identification and systematic analysis. Larval characters are summarized in Table 173 and below.

Psettodidae (Fig. 342).—Aboussouan's (1972c) description of preflexion larvae of *Psettodes bennetti* was based on five specimens, 4.4–5.7 mm in length. Leis and Rennis (1983) describe a series of five larval specimens of *Psettodes erumei,* 3.0–8.7 mm in length. The smallest specimen has a large yolk sac, the 6.0-mm larva is in mid-flexion and the largest specimen is undergoing eye migration. Larvae have: a deep, relatively thick body; large head with massive jaws that extend well beyond the rear margin of the eye and bear large, early-forming curved teeth; large eye; small preopercular spines; and 10 early-forming elongate dorsal rays. Dorsal and anal fin rays are all present at 6.0 mm but rays do not appear in paired fins until about 8.0 mm. Preflexion larvae have a series of large melanophores along the dorsal midline, large melanophores alternating with smaller ones

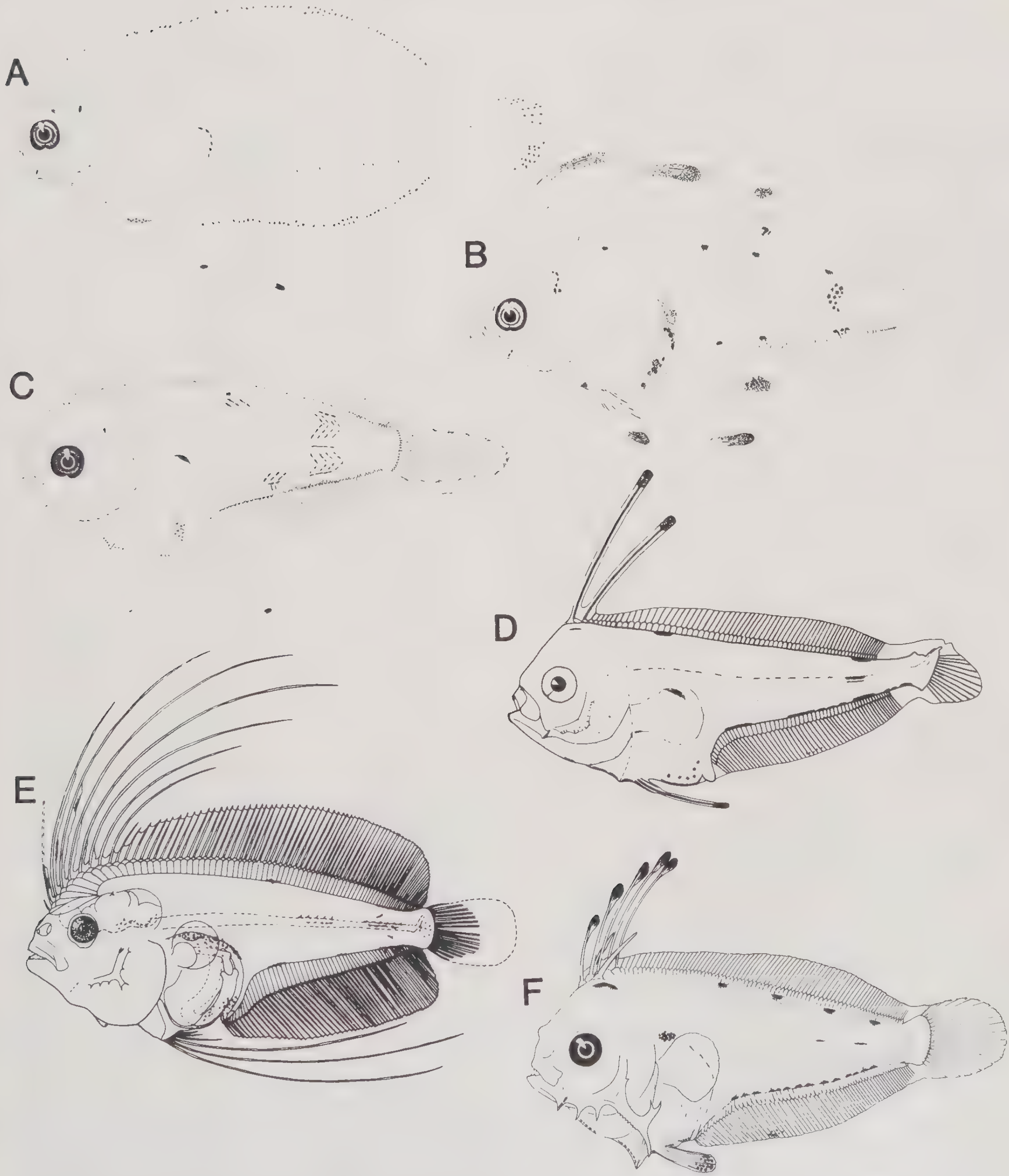


Fig. 345. Larvae of Paralichthyidae. (A) *Citharichthys stigmaeus,* 14.8 mm, from Ahlstrom and Moser, 1975; (B) *C. sordidus,* 14.5 mm, ibid; (C) *C. platophrys,* 8.6 mm, original, CalCOFI; (D) *Etropus crossotus,* 6.0 mm, from Tucker, 1982; (E) *Cyclopsetta chittendeni,* 13.0 mm, from Evseenko, 1982a; (F) *Syacium ovale,* 6.5 mm, original, CalCOFI.

TABLE 174. NUMBERS OF RAYS IN DORSAL CREST AND SIZE AT DEVELOPMENTAL EVENTS IN PARALICHTHYIDAE.

Species	Number of elongate dorsal fin rays	Size at hatching (mm)	Size at flexion (mm)	Size at transformation (mm)	References
Hippoglossina stomata	6	3.7	6.2–8.8	9.1–>11.7	Sumida et al., 1979
H. oblonga	~6	2.7–3.2	6.3–7.7	10–14	Leonard, 1971
Paralichthys californicus	5	2.0	6.0–7.3	7.5–9.4	Original, Ahlstrom and Moser, 1975
P. dentatus	4–8	2.4–2.8	7–9.5	~9.5	Smith and Fahay, 1970
P. olivaceus	5–6	2.6–2.8	7.1–8.7	10.2–>14.2	Okiyama, 1967
Xystreurys liolepis	6	2.0	6.0–6.7	7.5–>8.7	Original
Pseudorhombus elevatus	9	—	5.5–6.4	~10	Devi, 1969
P. pentophthalmus	7	—	7.1–7.6	8.7–12.2	Okiyama, 1974a; Minami, 1981a
Tarphops oligolepis	8	—	—	9.2–12.5	Okiyama, 1974a
Citharichthys arctifrons	3	<2.3	~5–8	13–15	Richardson and Joseph, 1973
C. cornutus	3	<2.2	5.8–8.9	~18	Tucker, 1982
C. gymnorhinus	3	—	5.3–7.7	~18	Tucker, 1982
C. platophrys	3	<2.0	5.3–6.1	11.2–18.5	Original
C. sordidus	2	~2.0	10.4–11.4	20–>39	Ahlstrom, 1965; original; Ahlstrom and Moser, 1975
C. spilopterus	2	—	5.7–6.8	9–12	Tucker, 1982
C. stigmaeus	0	~2.0	9.2–10.2	24.0–>35.5	Ahlstrom, 1965; original; Ahlstrom and Moser, 1975
Etropus crossotus	2	<2.3	4.9–9.5	~11	Tucker, 1982
E. microstomus	0	<2.3	5–7	10–12	Richardson and Joseph, 1973
Cyclopsetta chittendeni	8–9	—	~7.5	>13.0	Evseenko, 1982a
C. fimbriata	~9	~1.5	6.9	14.0	Gutherz, 1970; Evseenko, 1982a
C. querna	8–11	—	—	>32	Ahlstrom, 1972a
Syacium guineensis	7	<2.1	<6.5	>13.9	Aboussouan, 1968b
S. gunteri	5–8	<1.8	—	—	Evseenko, 1982a
S. micrurum	5–8	<1.8	—	—	Evseenko, 1982a
S. ovale	5–8	~1.6	4.1–4.8	~14–~20	Ahlstrom, 1972a; original
S. papillosum	5–8	<2.3	5.5–6.0	15–13	Futch and Hoff, 1971; Evseenko, 1982a

along the ventral midline, and small melanophores on the trunk, tail, ventral gut, pectoral fin, brain and lower jaw. During flexion the entire body except for the caudal fin base becomes solidly pigmented, a darker band forms forward of the caudal peduncle, and the snout becomes heavily pigmented.

Citharidae (Fig. 342).—Larvae of this family are known from five specimens (4.0–8.0 mm) of *Brachypleura novaezeelandiae* described by Pertseva-Ostroumova (1965). Notochord flexion occurs between 5.0 and 7.0 mm and transformation at about 8.0 mm. Larvae have a moderately deep, thick body and a large head with large jaws and eyes and about 10 large preopercular spines; the sixth dorsal ray is elongate and the rays anterior to it are assumed to be elongate, although damaged in all available specimens; pelvic fins are elongate, extending beyond the anus; pigment consists of a series of melanophores along the dorsum, a series along the horizontal septum, and a postanal series along the ventrum, melanophores below the gut, and on the pelvic fin.

Scophthalmidae (Fig. 343).—Larvae are known for 9 of the 10 species of this family. Petersen (1909) described 5 of the 7 species occurring in the eastern North Atlantic; Jones (1972) provided excellent illustrations of the 2 species of eastern Atlantic *Scophthalmus* and Bigelow and Welsh (1925) described larvae of *S. aquosus*, the only western Atlantic representative of the family. Newly hatched larvae are 2.0–4.0 mm in length (Table 171); size at notochord flexion for most species is 6.0–8.0 mm. Metamorphosis can begin by 8 or 9 mm and be completed by 13 mm (*S. aquosus, Phrynorhombus norvegicus, Zeugopterus punctatus*) or delayed to over 20 mm (*S. maximus, S. rhombus*). Larvae are deep- and thick-bodied, especially at the gut, have a large head and jaws and moderate to large eyes. Scophthalmid larvae develop extensive head spination. Three species (*Z. punctatus, P. regius, Lepidorhombus whiffiagonis*) develop paired otic spines. In *Z. punctatus*, spines also develop at the lateral aspect of the midbrain and on the opercle. Larvae of *P. norvegicus* develop spines along the lower jaw, on the opercle and preopercle, and at the shoulder (posttemporal region) while *L. boscii* has preopercular spines and a shoulder cluster. *S. maximus* and *S. rhombus* have a supraocular spiny ridge, numerous spines on the opercle and preopercle and a shoulder cluster. Pigmentation is heavy on the head and body in most species. *Z. punctatus* has a series of finfold bars and *L. boscii* develops these and also incomplete bars on the body. Late larvae of all species develop bars on the dorsal and anal fins.

Paralichthyidae (Figs. 344, 345).—Three subgroups are recognized in this family on the basis of adult characters: *Paralichthys* and relatives (*Ancylopsetta, Gastropsetta, Hippoglossina, Lioglossina, Verecundum, Xystreurys*); *Pseudorhombus* and relatives (*Cephalopsetta, Tarphops*); and *Cyclopsetta* and relatives (*Citharichthys, Etropus, Syacium*).

In the first group larvae are known for species of *Paralichthys* and *Hippoglossina* and for *Xystreurys liolepis* and in the second group larvae are known for *Pseudorhombus* and *Tarphops*. In

TABLE 175. MERISTIC AND LARVAL CHARACTERS OF BOTHIDAE.

Taxon	Larvae described[1]	Number of vertebrae	Urohyal spines[2]	Basipterygial spines	Cleithral spines	Otic spines	Scale spines	2nd dorsal ray[3]	Length at transformation (mm)	References
Taeniopsettinae										
Engyophrys	+	10 + 27–31 = 37–41	++	++	++	+	0	M	~19	Hensley, 1977
Taeniopsetta	+	10 + 30–32 = 40–42	++	++	++	+	0	S	~60	Amaoka, 1970
Trichopsetta	+	10–11 + 30–33 = 40–43	++	++	++	+	0	S	~28	Futch, 1977
Perissias	–	10 + 29–30 – 39–40								
Bothinae										
Arnoglossus	+	10–12 + 27–36 = 37–48	0	0	0	0	+	M, L	21–46	Kyle, 1913; Pertseva-Ostroumova, 1965; Amaoka, 1973, 1974
Bothus	+	10 + 25–32 = 35–42	0	0	0	0	0	M, L	9–42	Kyle, 1913
Chascanopsetta	+	16–18 + 37–44 = 53–59	0	0	0	0	0	M	78–120	Bruun, 1937; Nielsen, 1963b; Amaoka, 1971; Pertseva-Ostroumova, 1971
Crossorhombus	+	10 + 24–27 = 34–37	0	+	0	0	+	M, L	15–20	Ochiai and Amaoka, 1963
Engyprosopon	+	10 + 23–27 = 33–37	++	++	0, ++	0	0	M	16–18	Pertseva-Ostroumova, 1965
Grammatobothus	+	10 + 27–28 = 37–38	+	+	0	0	0	M	~15	
Kamoharaia	+	13–14 + 37–39 = 50–53	0	0	0	0	0	M	~91	Nielsen, 1963c
Laeops	+	10–12 + 35–42 = 46–53	0	0	0	0	0	L	51–80	Balakrishnan, 1963; Amaoka, 1972a; Hubbs and Chu, 1934
Lophonectes	+	10 + 32–33 = 42–43	0	+	0	0	0	M	~20	Original
Monolene	+	10 + 28–38 = 38–48	0	0	0	0	0	L	~30	Futch, 1971
Pelecanichthys	+	17 + 40 = 57	0	0	0	0	0	M	>90	Struhsaker, pers. comm.
Psettina	+	10 + 29–30 = 35–40	+	+	0	0	+	M	16–20	Pertseva-Ostroumova, 1965; Amaoka, 1976
Asterorhombus	–	10 + 26–27 – 36–37								
Japonolaeops	–	11 + 41–44 = 52–53								
Mancopsetta	–	13–16 + 38–50 = 52–66								
Neolaeops	–	13 + 38 = 51								
Parabothus		10 + 31–36 = 41–46								
Tosarhombus	–	10 + 28–30 – 38–40								

[1] + = yes; = no. [2] 0 = absent; + = present; ++ = strong

[3] S = short; M = moderate, L = long

these two subgroups hatching, notochord flexion and metamorphosis occur at a small size (Table 174). Larvae of these groups are noted for a dorsal crest consisting of elongate early forming rays, beginning with the second dorsal ray (Table 174). Larvae of the *Paralichthys* group are moderate in body depth, with a deep head and moderate-size jaws. Body thickness is moderate except that *Paralichthys* is more laterally compressed than in other genera reported (Fig. 344). The gut mass is large. Preopercular spination consists of an anterior and posterior series in *Paralichthys, Pseudorhombus* and *Tarphops* and an anterior series only in *Hippoglossina.* Larvae of *Paralichthys dentatus* have one to several minute sphenotic spines (Smith and Fahay, 1970) and *P. olivaceus* develops a spine cluster on the sphenotic, one spine on the epiotic, and 1–2 spines on each bone in the opercular series. Larvae of *Pseudorhombus pentophthalmus* have a single sphenotic spine, and some on the opercular bones (Okiyama, 1974a); Devi (1969) shows two rows of sphenotic spines in *P. elevatus.*

Yolk-sac larve of the *Paralichthys* and *Pseudorhombus* groups develop moderate to heavy pigmentation with some on the finfolds. Later-stage larvae have pigment over the brain, on the lower head and jaw region and below and lateral to the gut. Most species have a melanophore series along the dorsum and ventrum. Lateral pigment may consist of a series along the horizontal septum (*Paralichthys, Tarphops*), a wide-spread zone of melanophores (*Xystreurys, Hippoglossina*) or a posterior bar (*Pseudorhombus pentophthalmus*). Most species have a series of internal melanophores above the spinal column and some melanophores on the posterior region of the finfold and developing dorsal and anal fins.

Larvae of the *Cyclopsetta* assemblage are similar morphologically to those of the *Paralichthys* and *Pseudorhombus* assemblages, but differ in spination and fin ray development. The rays forming the dorsal crest are typically longer and stand out more abruptly compared with *Paralichthys* and associated genera. The fin ray complement of the crest, along with other characters, divides the assemblage into two generic pairs: *Citharichthys-Etropus* and *Cyclopsetta-Syacium.* Species of the former group have either two or three elongate rays, except for two species which lack a crest altogether (Table 174). Species of *Syacium* have 5–8 elongate dorsal rays and 8–11 occur in *Cyclopsetta.* The left pelvic fin forms before the right and may develop elongate rays in some species. The first two pelvic rays are elongate in *Citharichthys sordidus* and *C. platophrys,* the second ray only is elongate in *C. cornutus, C. gymnorhinus, C. spilopterus* and *Etropus crossotus*; *C. arctifrons, C. stigmaeus* and *E. micros-*

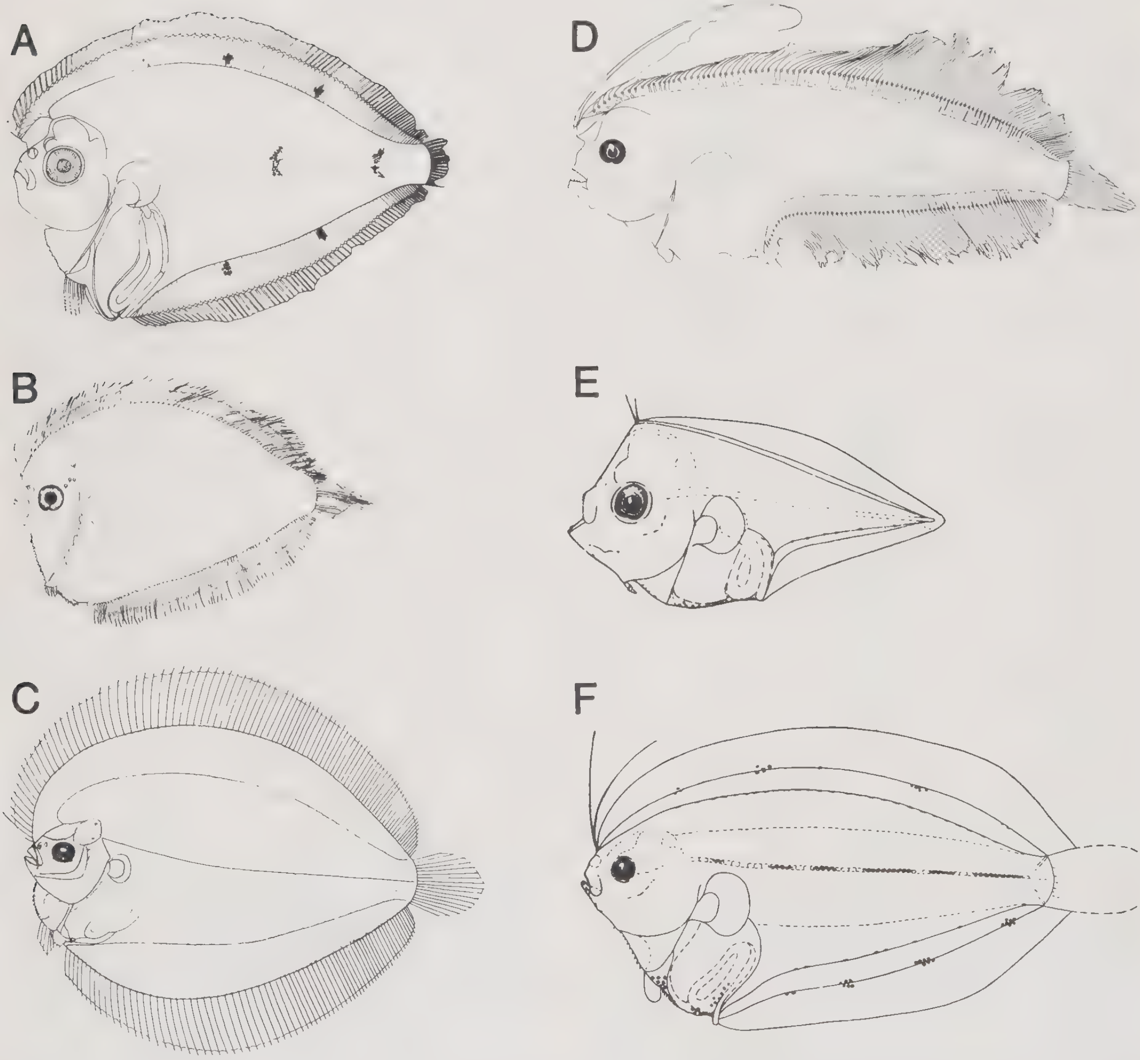


Fig. 346. Larvae of Bothidae. (A) *Trichopsetta ventralis,* 21.9 mm, from Evseenko, 1982a; (B) *Engyophrys senta,* 12.3 mm, from Hensley, 1977; (C) *Taeniopsetta ocellata,* 59.0 mm, from Amaoka, 1970; (D) *Monolene sessilicauda,* 14.3 mm, redrawn from Futch, 1971; (E) *Psettina hainanensis,* 4.2 mm, from Pertseva-Ostroumova, 1965; (F) *P. hainanensis,* 18.1 mm, ibid.

tomus lack elongate pelvic rays. The first three pelvic rays become markedly elongate in *Cyclopsetta* and the entire left fin becomes moderately elongate in *Syacium.*

Etropus and *Citharichthys* (except for *C. arctifrons*) develop one or more rows of small preopercular spines. According to Tucker (1982), small frontal-sphenotic spines are present in some species of *Citharichthys* and *Etropus* (6–8 spines on each side in *C. cornutus,* up to 6 in *C. gymnorhinus,* 1–2 in *C. spilopterus,* and 3–4 in *E. crossotus*). *Syacium* and *Cyclopsetta* develop a series of large preopercular spines at the margin of the bone and, in some species, an irregular anterior series. The spine at the angle of the primary series becomes antler-like in preflexion larvae of *Syacium* and in postflexion larvae of *Cyclopsetta.* Early preflexion larvae of *Syacium* develop single elongate sphenotic spines which remain prominent during the remainder of the larval period. Sphenotic spines in *Cyclopsetta* are early-forming but short.

Larvae of both subgroups of the *Cyclopsetta* assemblage typically have pigment above the brain, on the lower head region, below the gut, lateral to the posterior region of the gut, and above the gas bladder. Early preflexion larvae of most species have a series of small postanal melanophores and a bar or a

TABLE 176. SIZE DATA FOR PLEURONECTINAE LARVAE.

	Size at hatching (mm)	Size at notochord flexion (mm)	Size at transformation (mm)	References
Acanthopsetta nadeshnyi	<3.0	8.4–9.9	ca. 20–?	Pertseva-Ostroumova, 1961
Atheresthes evermanni	<8.4	ca. 11.5–15	—	Pertseva-Ostroumova, 1961
A. stomias	—	—	32.9–?	Pertseva-Ostroumova, 1961
Cleisthenes herzensteini	2.2–2.6	7.0–7.9	8.1–11.4	Okiyama and Takahashi, 1976; Dekhnik, 1959
Embassichthys bathybius	ca. 9.0	—	16.2–?	Richardson, 1981b
Eopsetta grigorjewi	2.5–3.0	7.2–8.9	11.4	Okiyama and Takahashi, 1976
E. jordani	2.8	—	—	Alderdice and Forrester, 1971
Glyptocephalus cynoglossus	3.5–5.6	15–21	25–?	Petersen, 1904
G. stelleri	4.1–5.2	15–17	19–48	Okiyama, 1963; Dekhnik, 1959; Pertseva-Ostroumova, 1961
G. zachirus	ca. 6	15.3–24.0	49–72	Original; Ahlstrom and Moser, 1975
Hippoglossoides dubius	3.0–3.4 TL	<12.4	18.1	Okiyama and Takahashi, 1976
H. elassodon	5.4–6.6 TL	9.0–10.2	—	Dekhnik, 1959; Pertseva-Ostroumova, 1961
H. platessoides	4.0–6.0	9.5–17.5	18–30	Petersen, 1904; Russell, 1976; Nichols, 1971; Colton and Marak, 1969
H. robustus	ca. 4.0	ca. 11–?	>28.6	Pertseva-Ostroumova, 1961
Hippoglossus hippoglossus	6.5–7.0	16–18	22–34	Schmidt, 1904; Russell, 1976 (summary)
H. stenolepis	7.8–8.5	13.6–17.8	14.7–24.1	Thompson and Van Cleve, 1936; Pertseva-Ostroumova, 1961
Hypsopsetta guttulata	1.7–2.3	4.0–5.2	4.4–>8.8	Sumida et al., 1979
Isopsetta isolepis	2.7–2.9	9.1–14.0	15–>21.9	Richardson et al., 1980
Kareius bicoloratus	ca. 3.0	ca. 4.0–9.0	ca. 14–?	Pertseva-Ostroumova, 1961
Lepidopsetta bilineata	3.4–3.8	ca. 8.4–9.9	>17.7	Pertseva-Ostroumova, 1961
L. mochigarei	3.95–4.48	ca. 8.9	—	Yusa, 1958; Okiyama and Takahashi, 1976
Limanda aspera	2.2–2.8	7.5–9.5	ca. 10–?	Dekhnik, 1959; Pertseva-Ostroumova, 1961
L. ferruginea	2.0–3.5	5.9–ca. 10	ca. 14	Bigelow and Welsh, 1925; Miller, 1958
L. limanda	2.7–4.0	7–8.7	12–20	Russell, 1976 (summary)
L. punctatissima	1.79–2.21	—	8.1–>9.6	Pertseva-Ostroumova, 1961
L. schrenki	ca. 2.4	—	—	Hikita, 1952
L. schrenki (as *Pseudopleuronectes yokohamae*)	ca. 2.4	<7.4	12.0–?	Pertseva-Ostroumova, 1961
L. yokohamae	3.5–3.8	ca. 7.0	ca. 7.5–10.0	Yusa, et al., 1971; Minami, 1981a
Liopsetta glacialis	3.7	—	—	Pertseva-Ostroumova, 1961
L. obscura	2.5–3.5	~6.6	>9.0	Pertseva-Ostroumova, 1961; Kurata, 1956
L. pinnifasciata	3.15–3.93	8.11–8.45	>8.5	Pertseva-Ostroumova, 1961
L. putnami	3.1–3.6	6.0–7.1	7.3	Laroche, 1981
Lyopsetta exilis	ca. 5.6	9.0–10.9	15.7–24.7	Original; Ahlstrom and Moser, 1975
Microstomus achne	—	8.8	—	Okiyama and Takahashi, 1976
M. kitt	4.84	12–15	18–28	Petersen, 1904
M. pacificus	ca. 6.0	ca. 10–15	ca. 20–>45	Original; Ahlstrom and Moser, 1975
Parophrys vetulus	2.3–2.8	8.8–10.5	ca. 20	Original; Budd, 1940; Ahlstrom and Moser, 1975
Platichthys flesus	2.25	5.9–7.1	9–12	Nichols, 1971; Russell, 1976 (summary)
P. stellatus	1.9–2.1	5.5–6.0	—	Orcutt, 1950; Yusa, 1957; Pertseva-Ostroumova, 1961
P. pallasii (as *Platessa quadrituberculata*)	5.6	8.9	ca. 10.0–?	Pertseva-Ostroumova, 1961
P. platessa	6.0–7.5	8.9–10.2	10.5–14	Nichols, 1971; Russell, 1976 (summary)
Pleuronichthys coenosus	3.9	6.2–8.5	8.2–>11.4	Sumida et al., 1979; Budd, 1940
P. cornutus	2.65–2.8	>3.6	7.25–13.0	Takita and Fujita, 1964; Minami, 1982a
P. decurrens	4.9–5.5	7.8–11.0	10.5–>21.0	Sumida et al., 1979; Budd, 1940
P. ritteri	2.1	4.3–5.6	6.0–>10.0	Sumida et al., 1979
P. verticalis	2.4	5.0–7.2	7.3–>11.0	Sumida et al., 1979; Ahlstrom and Moser, 1975; Budd, 1940
Psettichthys melanostictus	<3.0	ca. 8.0	>22.6	Hickman, 1959
Pseudopleuronectes americanus	2.3–3.5	5.0–7.1	6.8	Breder, 1923; Laroche, 1981
P. herzensteini	2.6–2.9	ca. 6.0–8.5	ca. 10.4–?	Dekhnik, 1959
Reinhardtius hippoglossoides	10–16	25–27	45–65	Jensen, 1935
Tanakius kitaharai	ca. 3.0	—	18.9–ca. 20	Okiyama and Takahashi, 1976
Verasper variegatus	3.8	ca. 9–12.4	ca. 16.4–?	Takita et al., 1967; Pertseva-Ostroumova, 1961; Uchida, 1933

short lateral pigment series posteriad on the tail. In some species of *Citharichthys* the ventral series coalesces into a more sparse series of larger spots and a similar series develops along the dorsum (e.g., *C. arctiforns, C. cornutus, C. sordidus*). In other species, series along the dorsum and ventrum are abbreviated or absent and only the tail bar may be present (e.g., *C. gymnorhinus, C. platophrys*) or absent (*C. spilopterus*). *Etropus* larvae have dorsal and ventral series and either a short lateral series (*E. crossotus*) or a long one (*C. microstomus*). *Cyclopsetta* and *Syacium* have dorsal and ventral series and a short lateral series posteriad on the tail. Fin pigment is principally on the spatulate tips of the elongate dorsal and pelvic fin rays. Late-

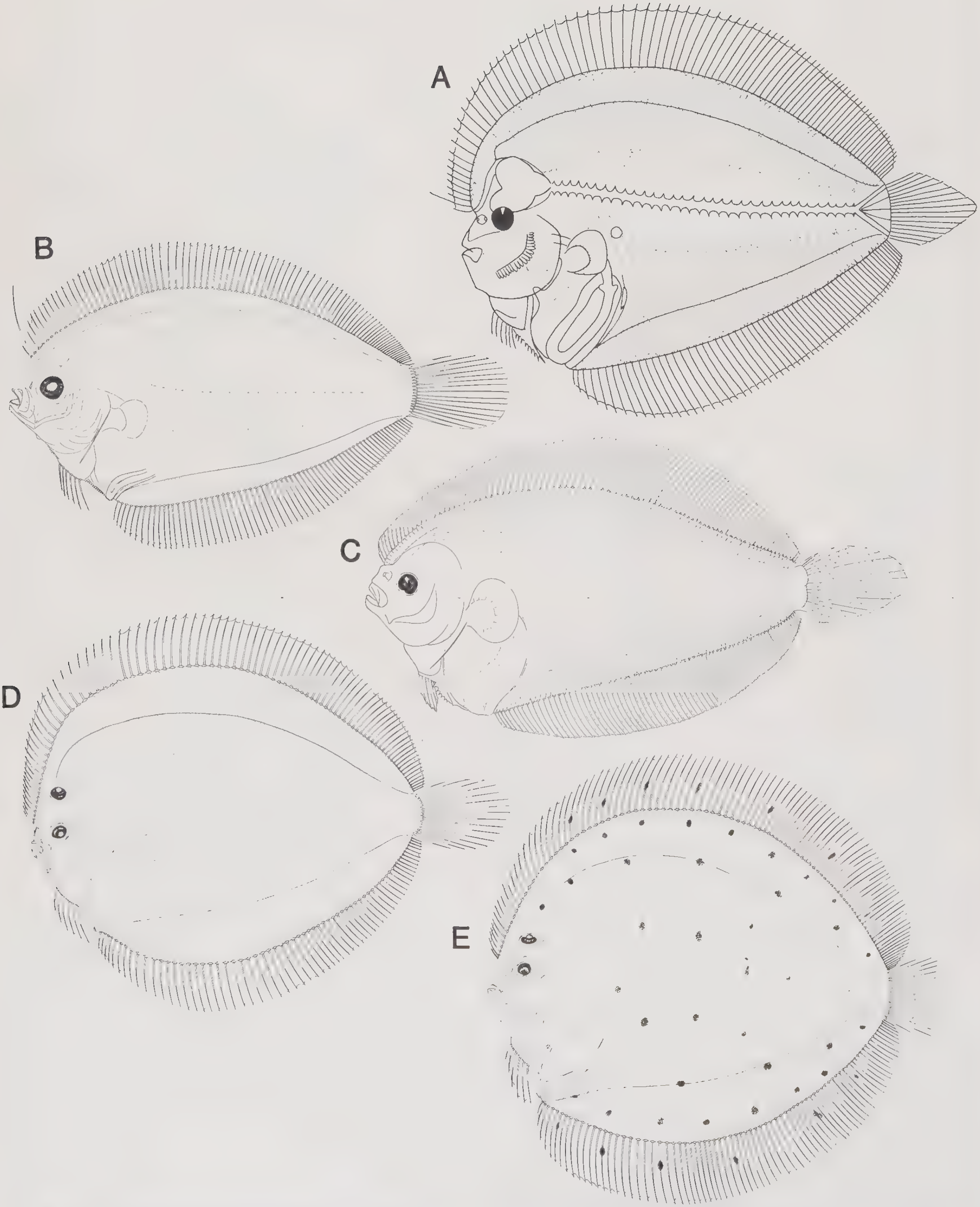


Fig. 347. Larvae and transforming specimens of Bothidae. (A) *Crossorhombus kobensis,* 16.0 mm, from Amaoka, 1979; (B) *Engyprosopon xenandrus,* ca. 20.0 mm; (C) *Lophonectes gallus,* 18.5 mm, original, K 138/74, New Zealand; (D) *Bothus thompsoni,* ca. 36.0 mm; (E) *B. mancus,* ca. 30.0 mm. B, D, and E from P. Struhsaker, unpublished.

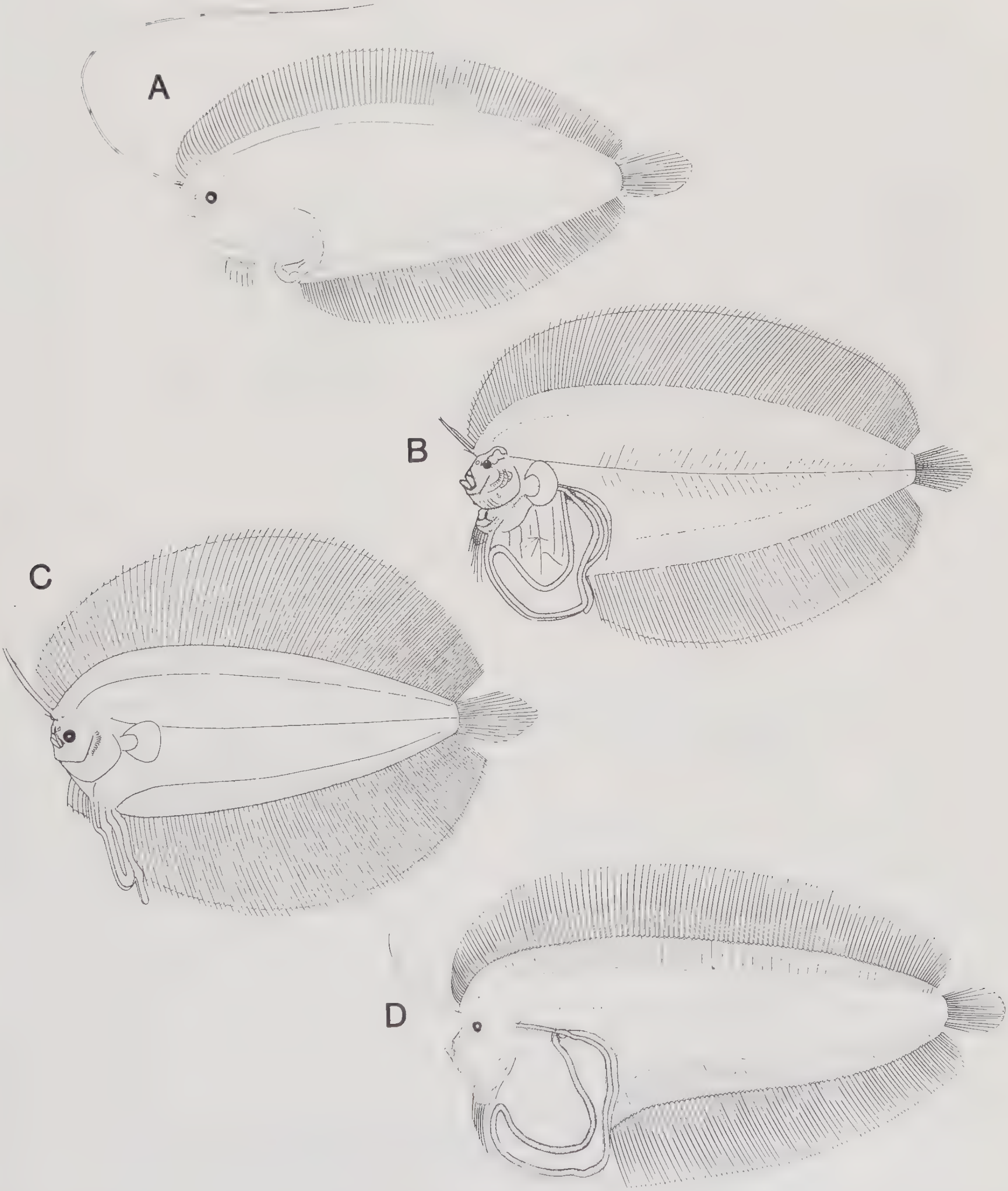


Fig. 348. Larvae of Bothidae. (A) *Arnoglossus debilis,* ca. 59.0 mm, from P. Struhsaker, unpublished; (B) *Chascanopsetta lugubris,* 120.0 mm, from Amaoka, 1971; (C) *Laeops kitaharae,* 79.0 mm, from Amaoka, 1972; (D) *Pelecanichthys* sp., ca. 95.0 mm, from P. Struhasker, unpublished.

TABLE 177. SIZE DATA FOR LARVAE OF ACHIRINAE AND SOLEINAE.

Taxon	Size at hatching (mm)	Size at flexion (mm)	Size at transformation (mm)	References
Achirinae				
Achirus lineatus	1.6	ca. 2.5–3	3.0–5.5	Houde et al., 1970
Trinectes maculatus	1.7–1.9	ca. 3–4	ca. 5	Hildebrand and Cable, 1938
Soleinae				
Aesopia cornuta	4.1	—	9.2–?	Mito, 1963
Austroglossus microlepis	1.7	5.5–6.6	8.5–ca. 16	O'Toole, 1977; Brownell, 1979
Bathysolea profundicola	—	—	4.32	Aboussouan, 1972c
Buglossidium luteum	1.8–2.3	ca. 6–8	ca. 6–10	Holt, 1891; Ehrenbaum, 1897
Dicologoglossa cuneata	1.3	ca. 6.3–6.5	7–7.5	Lagardere, 1980; Lagardere and Aboussouan, 1981
Euryglossa pan	<2.66	<4.6	3.4–6.5	Jones and Menon, 1951
Heteromycteris capensis	1.7	?–6.5	ca. 6.2–?	Brownell, 1979
H. japonicus	—	ca. 4.55	5.0–7.0	Minami, 1981b
Microchirus boscanion	—	—	7.2	Aboussouan, 1972c
M. frechkopi	—	—	5.68	Aboussouan, 1972c
M. ocellatus	2.0	4.6–5.1	6.8–>8.2	Palomera and Rubies, 1977
M. variegatus	2.4–2.9	6.1–>7.1	ca. 7–12 (18)	Cunningham, 1890; Petersen, 1909
Pegusa cadenati	—	—	7.0	Aboussouan, 1972c
P. impar	—	—	8.5–>12	Padoa, 1956k
P. lascaris lascaris	<3.5	5.3–8.1	9.5–>11.2	Clark, 1914
P. lascaris nasuta	2.1–2.5	—	—	Dekhnik, 1973; Padoa, 1956k
Solea cuneata	—	—	7.0	Aboussouan, 1972c
S. heinii	<2.2	>2.7–3.2	—	Balakrishnan and Devi, 1974
S. hexophthalma	—	—	8.0	Aboussouan, 1972c
S. ovata	—	ca. 3–4	4.5–?	Balakrishnan, 1963
S. solea	2.5–3.8	5.5–?	ca. 7–14.6	Russell, 1976 (summary)
Synaptura kleini	3.0	?–6.5	ca. 7–9	Brownell, 1979
Zebrias japonicus	4.1 TL	—	—	Mito, 1963
Z. zebra	4.0 TL	—	—	Mito, 1963

stage larvae of most species develop chevron-shaped bars on the epaxial and hypaxial myosepta. Metamorphosing specimens of *Cyclopsetta* have series of large ocelli on the dorsal and anal fins. *Dorsopsetta norma* described by Nielsen (1963b) on the basis of two metamorphosing specimens is apparently a species of *Cyclopsetta.*

Bothidae (Figs. 346–348).—Two bothid subfamilies are recognized, Taeniopsettinae and Bothinae. Bothid larvae are thin-bodied to diaphanous, sparsely pigmented, and all develop an elongate second dorsal ray (Table 175). Also, spines may appear on the urohyal, basipterygia, cleithra and epiotics in a pattern which is generally consistent for subfamilies and genera (Table 175). Bothid larvae reach a relatively large size before metamorphosis. Early larval stages are often poorly represented in collections.

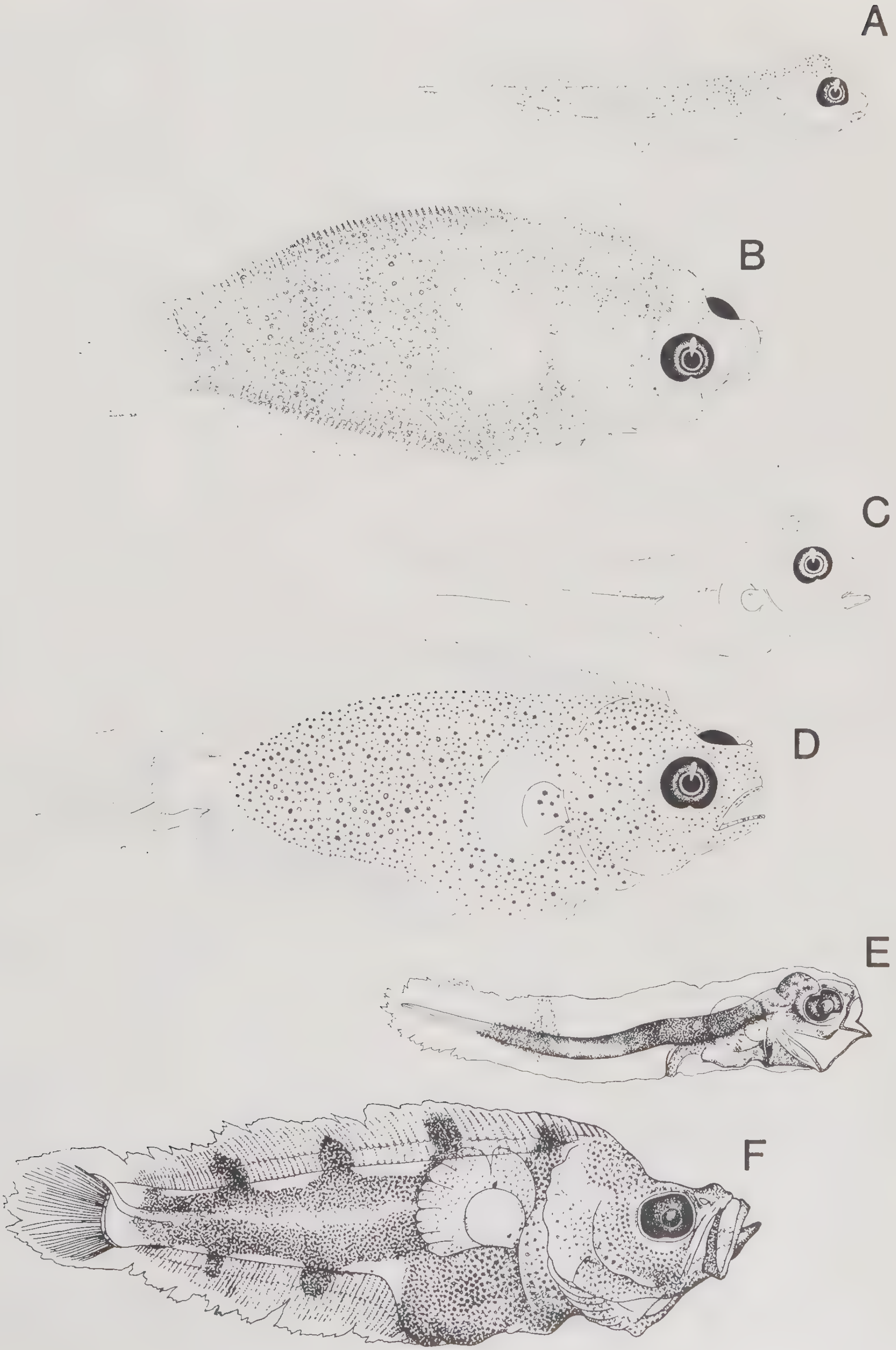
Larval series are known for all taeniopsettine genera, except *Perissias.* Larvae of *Trichopsetta* and *Engyophrys* are ovate while those of *Taeniopsetta* are round (Fig. 346). All have a complete complement of head spines (Table 175). The second dorsal fin ray is slightly or moderately elongate. *Taeniopsetta* lacks melanophores, but live larvae have four reddish-orange spots along the bases of the dorsal and anal fins, and orange, reddish and yellow blotches and bands on the body and head. *Trichopsetta* has three series of melanistic blotches along the dorsal and anal pterygiophores and along the body axis (left side). *Engyophrys* lacks melanophores.

Larvae of Bothinae have an ovate, round, or elongate shape Figs. 347, 348) and lack epiotic spines. *Engyprosopon* has numerous urohyal and basipterygial spines and some species have numerous spines on the cleithrum. *Psettina* and *Grammatobothus* have urohyal and basipterygial spines, and early larvae of the former have a hook-like projection on the lower jaw (Fig. 346). *Crossorhombus* and *Lophonectes* have basipterygial spines only and all other known bothid larvae lack head spines. *Crossorhombus* larvae have a series of scale spines along the bases of the dorsal and anal fins, one scale per ray, and species of *Psettina* and *Arnoglossus* also develop such scale spines. In the species of *Arnoglossus* described by Kyle (1913), patches of scale spines develop on the median and ventral regions of the abdomen. The second dorsal ray is usually moderately elongate but can be greatly elongate and ornamented, as in *Arnoglossus.*

Pigmentation is sparse in most bothine larvae and lacking in some species. Exceptions are found in species of *Arnoglossus* and *Psettina* which usually have melanophores above the brain, ventrally on the gut, above the gas bladder, in series along the dorsal and ventral midlines, and along the horizontal septum; in some species a complete or partial bar is present posteriad on the tail. Preflexion larvae of *Bothus* have a melanistic blotch near the tip of the notochord; later larval stages are unpigmented, except that transforming specimens of some species, *B. myriaster* (Amaoka, 1964) and *B. mancus* (Fig. 347), become heavily spotted over the body and fins. *Laeops* has melanistic blotches forming an irregular pattern over the body and median fins.

Monolene shares some adult characters with taeniopsettines but larval characters place it with the bothines. Larvae are elongate, lack head spines, have an elongate ornamented second dorsal ray, and melanistic pigment above the gut, on the right side of the brain and on the dorsal fin membrane (Fig. 346).

Pleuronectidae (Figs. 349–355).—Of the five pleuronectid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subfamilies recognized (see introduction), the Pleuronectinae is the largest with 26 genera, representing ⅔ of the genera in the family. Three contributions that summarize egg and larval information for pleuronectine flatfishes from the eastern North Atlantic and Mediterranean are Ehrenbaum (1905–1909), Padoa (1956k), and Nichols (1971). Bigelow and Welsh (1925), Bigelow and Schroeder (1953), Martin and Drewry (1978), and Fahay (1983) give information on eggs and larvae of western Atlantic pleuronectine flatfishes. The most comprehensive work dealing with early life history stages of flatfishes from the western North Pacific is Pertseva-Ostroumova (1961).

Yolk-sac larvae of pleuronectine flatfishes can be as small as 1.7 mm (*Hypsopsetta guttulata*) or as large as 10–16 mm (*Reinhardtius hippoglossoides*) and size at hatching is a primary character for identifying yolk-sac larvae (Table 176). The pigment pattern can be quite distinctive, as for example in the genus *Pleuronichthys*, but in many pleuronectines the body pigment migrates during the yolk-sac stage, and is variable from specimen to specimen of the same species. The yolk sac itself can lack pigment (as in *Parophrys vetulus, Hippoglossus stenolepis* or *Eopsetta jordani*), can be moderately pigmented (as in *Lyopsetta exilis, Lepidopsetta bilineata* or *Psettichthys melanostictus*) or can be heavily pigmented (as in *Pleuronichthys decurrens* or *Verasper variegatus*). Similarly the finfold can lack pigment or be variously pigmented and useful in identification.

Early preflexion pleuronectine larvae are slender; the head is of moderate size; snout-anus length can be as much as 50% NL (as in four species of *Pleuronichthys* larvae, Sumida et al., 1979) but usually is shorter (i.e., 35–45% NL). The gut is initially straight but develops a coil soon after the completion of yolk absorption. Greatest body depth after the gut becomes looped is either at the anus or slightly anterior to it. Body shape of preflexion larvae is quite similar from species to species. There are few distinctive characters unique to the larval period of pleuronectine flatfishes. Only a few kinds of pleuronectine larvae develop head spination. Preopercular spines form in larvae of *Atheresthes, Glyptocephalus, Tanakius* and *Eopsetta*; otic spines develop on larvae of *Microstomus* (at least on 2 species), *Hypsopsetta*, and *Pleuronichthys* (1 species); *Atheresthes* has a spinous supraocular crest. Head spination develops during the preflexion stage, but usually is best developed on flexion or early postflexion larvae.

The caudal fin begins forming either slightly before or together with the dorsal and anal fins. The first caudal supporting bones to form as cartilage are the hypurals. Usually several caudal rays (2 + 2 or 3 + 3) are formed before flexion begins. In late flexion and early postflexion larvae, the end of the notochord can project beyond the hypural plates. The complete complement of caudal rays is usually laid down during the flexion period.

The dorsal and anal fins form in the finfold at some distance from the main part of the body. The intervening space becomes filled with the pterygiophores that support the dorsal and anal fin rays, causing an increase in body depth. In both dorsal and anal fins the rays begin forming at the anterior ends of the fins and the differentiation proceeds posteriad. The first few rays in both fins are reduced in size and the terminal ray is often minute. Pelvic fin buds usually form during the flexion stage but pelvic rays usually are not developed until the postflexion stage. As in all flatfishes, formation of pectoral fin rays is delayed to the end of the transformation stage.

The vertebral processes ossify before the centra. In the caudal group of vertebrae, ossification of haemal and neural processes proceeds posteriad. Ossification of abdominal neural processes can follow several patterns, but usually proceeds anteriad. The last neural and haemal processes to ossify are the truncate spines of the 2 or 3 vertebrae anterior to the urostyle. Centra ossify initially at the bases of neural and haemal processes and ossification proceeds peripherally until a complete ring is formed. On first formation only the middle portion of a vertebral centrum is ossified, hence the space between adjacent centra may be as wide as the ossified portions of the centra. The ural centra are the first to ossify in some pleuronectines or they can ossify at the same time as other centra. The last centra to form are those of the 2 (or 3) vertebrae anterior to the urostyle.

All pleuronectine larvae that have been described have body pigment. The pigment pattern changes with growth, often markedly. Also, there is often considerable variation in pigmentation of larvae of similar sizes of the same species. Notwithstanding, body and finfold pigment constitutes a primary character for identification of flatfish larvae during the preflexion stage.

To show the variety of pigment patterns found on preflexion stage pleuronectine larvae, preflexion larvae of 17 species from the North Pacific are illustrated (Figs. 349–351). Heavily pigmented larvae are in the genera *Pleuronichthys, Hypsopsetta*, and *Verasper* (Fig. 349). The posterior portion of the tail is unpigmented or pigment is confined to marginal spots along the notochord. The unpigmented tail area is more extensive in some species than in others. Finfold pigment is very useful in identifying these larvae to species taken in conjunction with larval size and extent of tail pigment.

In the other 14 kinds of larvae representing as many genera, tail pigment appears in a number of patterns. The larvae illustrated in Figs. 350 and 351 are arranged in the order of increasing complexity. In the simplest pattern pigment is concentrated along the ventral midline with only moderate dorsal or lateral pigment, as in *Hippoglossus stenolepis* or *Reinhardtius hippoglossoides.* Although *Parophrys vetulus* and *Lyopsetta exilis* have more ventral margin pigment than dorsal, it is almost continuous on both margins. *Platichthys stellatus* has more diffused pigment over the tail portion of the body, but it is not in a pattern. The most unusual pigment is found in *Atherestes.* There are two conspicuous dorsal patches as opposed to almost no ventral pigment. Pigment on *Eopsetta jordani* is limited to a mid-tail band and a terminal notochord patch. A more common pattern is encountered in *Isopsetta*, which has two pigment bands across the tail together with the terminal notochord pigment. A basically similar pattern is found in *Lepidopsetta bilineata. Psettichthys* is unusual in having alternating dorsal and ventral blotches. *Hippoglossoides elassodon* has three tail pigment areas (i.e., opposing dorsal and ventral pigment patches) together with terminal notochord pigment. This is also the basic pattern in *Microstomus. Embassichthys* increases opposing tail patches to

Fig. 349. Larvae and transforming specimens of Pleuronectidae. (A) *Pleuronichthys coenosus*, 3.7 mm, from Sumida et al., 1979; (B) *P. coenosus*, 8.9 mm, ibid; (C) *Hypsopsetta guttulata*, 2.6 mm, ibid; (D) *H. guttulata*, 6.6 mm, ibid; (E) *Verasper variegatus*, 5.6 mm, from Pertseva-Ostroumova, 1961 after Uchida, 1933; (F) *V. variegatus*, 12.4 mm, ibid.

four plus terminal notochord pigment (Richardson, 1981b); *Glyptocephalus zachirus* has pigment bands which alternate with ventral patches, plus the terminal notochord pigment.

At least four other genera of pleuronectine flatfishes occur in the eastern North Pacific. The preflexion stage larvae of *Pleuronectes pallasii, Liopsetta glacialis,* and *Limanda aspera* lack melanistic bands (Pertseva-Ostroumova, 1961). Larvae are unknown for the fourth genus, *Clidoderma.*

Larvae are known for species representing six additional genera in the western North Pacific. According to Pertseva-Ostroumova (1961), preflexion larvae of *Acanthopsetta nadeshnyi* and *Kareius bicoloratus* lack bands; those of *Cleisthenes herzensteini* (see also Okiyama and Takahashi, 1976), *Pseudopleuronectes herzensteini* and *P. yokohamae* (see also Dekhnik, 1959; Yusa, 1960a, b; Yusa et al., 1971) have two tail pigment bands plus terminal notochord pigment. Preflexion larvae of *Verasper variegatus* (Fig. 349) are as heavily pigmented as those of *Pleuronichthys* (Takita et al., 1967; Uchida, 1933). The pigment pattern on preflexion larvae of *Tanakius kitaharai* is very similar to that on larvae of *Glyptocephalus stelleri* (Okiyama and Takahashi, 1976). Larvae have not been described for the monotypic genus *Dexistes.*

In species with banded preflexion larvae, the bands usually persist into later larval stages; those with diffuse or linear pigment patterns generally do not develop bands in later stages, although pigment may become associated with myosepta (Figs. 352, 353). Virtually all late postflexion and metamorphic pleuronectines develop a distinct pattern of bars or blotches on the body and median fins, which persists into the juvenile stage (Fig. 354).

Of the four other pleuronectid subfamilies, larvae have not been described for Paralichthodinae, while some information is available on the Samarinae, Poecilopsettinae, and Rhombosoleinae. Pertseva-Ostroumova (1965) described two larval specimens (6.4, 8.7 mm) of *Samaris cristatus* and Struhsaker (pers. comm.) has described large pelagic larvae of *Samariscus* sp. and *Poecilopsetta hawaiiensis* (Fig. 355). Larvae of *S. cristatus* are deep-bodied in the gut region, have a relatively large head and jaws and a pigment pattern consisting of melanophore patches along the dorsum and ventrum, along the outer margins of the pterygiophore zones, and along the dorsal and anal fins; the ventral region of the gut is pigmented. A series of *Samariscus triocellatus,* 7.3–19.0 mm (provided by Dr. T. A. Clarke, Univ. of Hawaii), is similar to *Samaris cristatus* in having a slender body and wide pterygiophore zones but the gut coil is elongate, protrudes beyond the ventral profile, and the fourth dorsal ray is elongate. The left eye has begun to migrate at 7.3 mm and is at the dorsal midline by 12.0 mm. Larvae of *Samariscus corallinus* are similar but attain a larger size (ca. 26 mm). Both species lack pigment. Late postflexion larvae of *Poecilopsetta* have a body form similar to samarines (slender body with wide pterygiophore zones) but have a different gut structure, no elongate dorsal ray, and have a striking pigment pattern consisting of dorsal and ventral myoseptal series and large blotches over the pterygiophore zones, dorsal and anal fins, and gut (Fig. 355). A 29-mm late postflexion larva from the North Atlantic has a pigment pattern identical to Hawaiian specimens.

Reared yolk-sac and early preflexion larvae of rhombosoleine species have been illustrated and briefly described: *Ammotretis rostratus* (Thomson, 1906); *Rhombosolea plebeia* (Anderton, 1907); *Colistium guntheri, Pelotretis flavilatus,* and *Peltorhamphus novaezeelandiae* (Thomson and Anderton, 1921). The oil globules remain evenly dispersed throughout the yolk-sac period. Heavy melanistic pigmentation develops on the head, body, yolk sac, and finfold. Late yolk-sac larvae of *C. guntheri* develop an unusual lobate projection of the dorsal finfold, which extends well anterior to the head. A similar structure appears in yolk-sac larvae of the soleid, *Pegusa lascaris* (Holt, 1891). Rapson (1940) described and illustrated with photographs a reared series of *Pelotretis flavilatus.* Flexion-stage larvae of this species are deep-bodied and similar in appearance to paralichthyids, although they lack elongate dorsal fin rays (Fig. 355). Pigmentation consists of dorsal and ventral midline series, series above and below the spinal column, a linear patch below the gut, and embedded melanophores in the otic region. Postflexion larvae become mottled with large blotches on the body and fins. Crossland (1981) briefly described and illustrated pre- and postflexion stages of a similar larva which he identified as *Peltorhamphus latus* and stated that Rapson's (1940) series was a species of *Peltorhamphus.* Crossland's (1982) illustration of a flexion-stage *Pelotretis flavilatus* has heavy pigmentation, a protruding gut mass and looks very much like a soleid.

Soleidae (Fig. 356).—Two subfamilies, Soleinae and Achirinae, are recognized in the family. In the Soleinae, life history stages are well known for the eastern North Atlantic species, *Solea solea, Microchirus variegatus, Buglossidium luteum* and *Pegusa lascaris* (references summarized in Ehrenbaum, 1905–1909 and Russell, 1976). A comprehensive volume on the development of *S. solea* was produced by Fabre-Domergue and Biétrix (1905). Padoa (1956k) summarized information on eggs and larvae of soles from the Mediterranean, and Aboussouan (1972c) briefly

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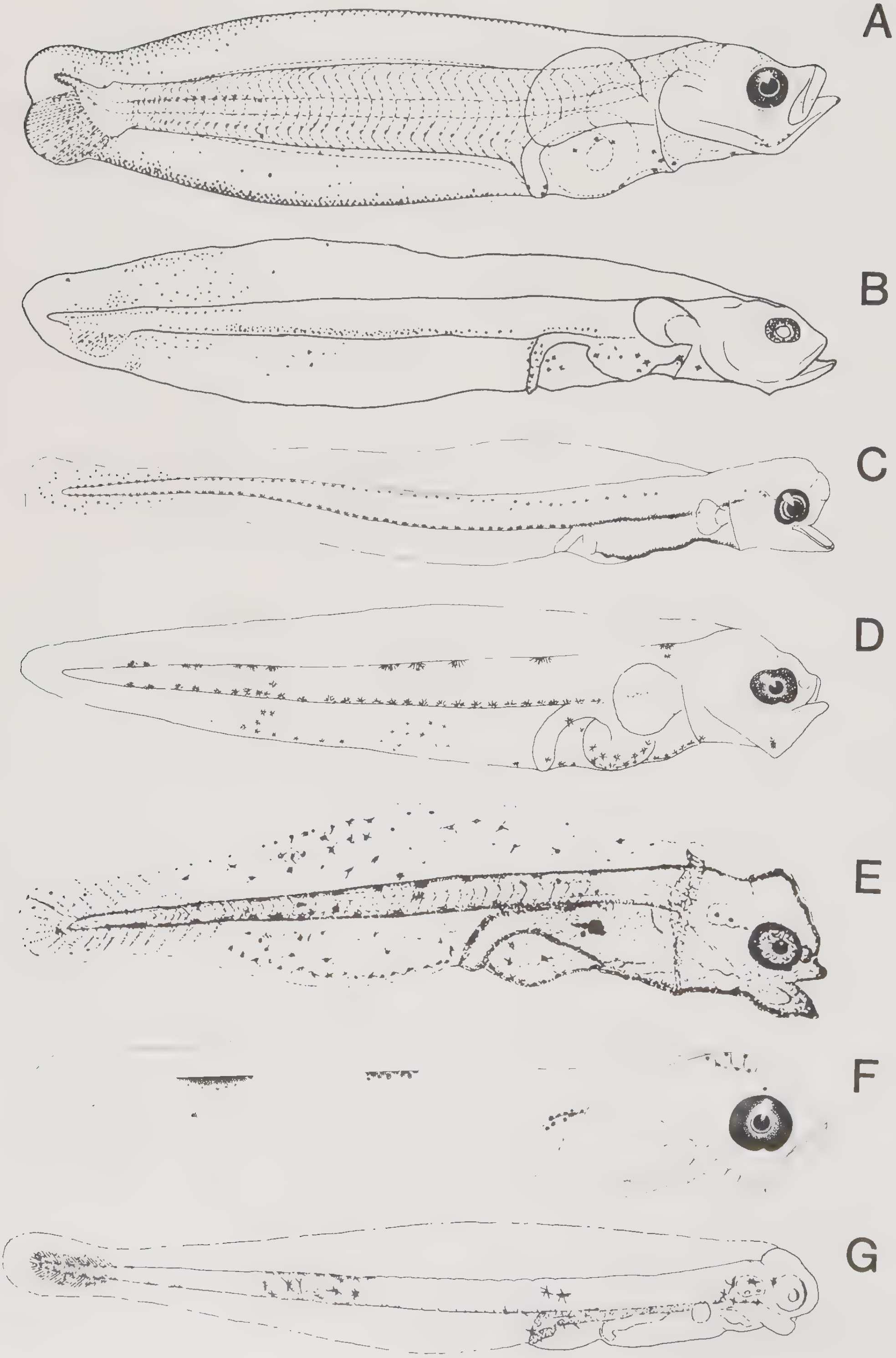
Fig. 350. Larvae of Pleuronectidae. (A) *Hippoglossus stenolepis,* 15.0 mm, from Pertseva-Ostroumova, 1961; (B) *Reinhardtius hippoglossoides,* 17.0 mm, from Jensen, 1935; (C) *Lyopsetta exilis,* 5.9 mm from Ahlstrom and Moser, 1975; (D) *Parophrys vetulus,* 4.3 mm, ibid; (E) *Platichthys stellatus,* 2.6 mm, from Orcutt, 1950; (F) *Atheresthes stomias,* 10.5 mm, original; (G) *Eopsetta jordani,* 6.2 mm, from Alderdice and Forrester, 1971.

Fig. 351. Larvae of Pleuronectidae. (A) *Isopsetta isolepis,* 9.5 mm, original, CalCOFI 7205, Sta. 40.38; (B) *Lepidopsetta bilineata,* 4.6 mm, from Pertseva-Ostroumova, 1965; (C) *Psettichthys melanostictus,* 6.7 mm, original, CalCOFI 5807 Sta. 40.38; (D) *Hippoglossoides elassodon,* 9.2 mm, from Pertseva-Ostroumova, 1961; (E) *Microstomus pacificus,* 7.0 mm, redrawn from Ahlstrom and Moser, 1975; (F) *Embassichthys bathybius,* 18.5 mm, original, CalCOFI 4905, Sta. 29.83; (G) *Glyptocephalus zachirus,* 22.8 mm, redrawn from Ahlstrom and Moser, 1975.

Fig. 352. Larvae of Pleuronectidae. (A) *Lyopsetta exilis,* 14.7 mm, original, CalCOFI 7805, Sta. 100.29; (B) *Parophrys vetulus,* 16.0 mm, redrawn from Ahlstrom and Moser, 1975; (C) *Isopsetta isolepis,* 14.2 mm, original, CalCOFI 7205, Sta. 40.38, (D) *Eopsetta grigorjewi,* 10.0 mm, from Okiyama and Takahashi, 1976; (E) *Psettichthys melanostictus,* 9.4 mm, original, CalCOFI.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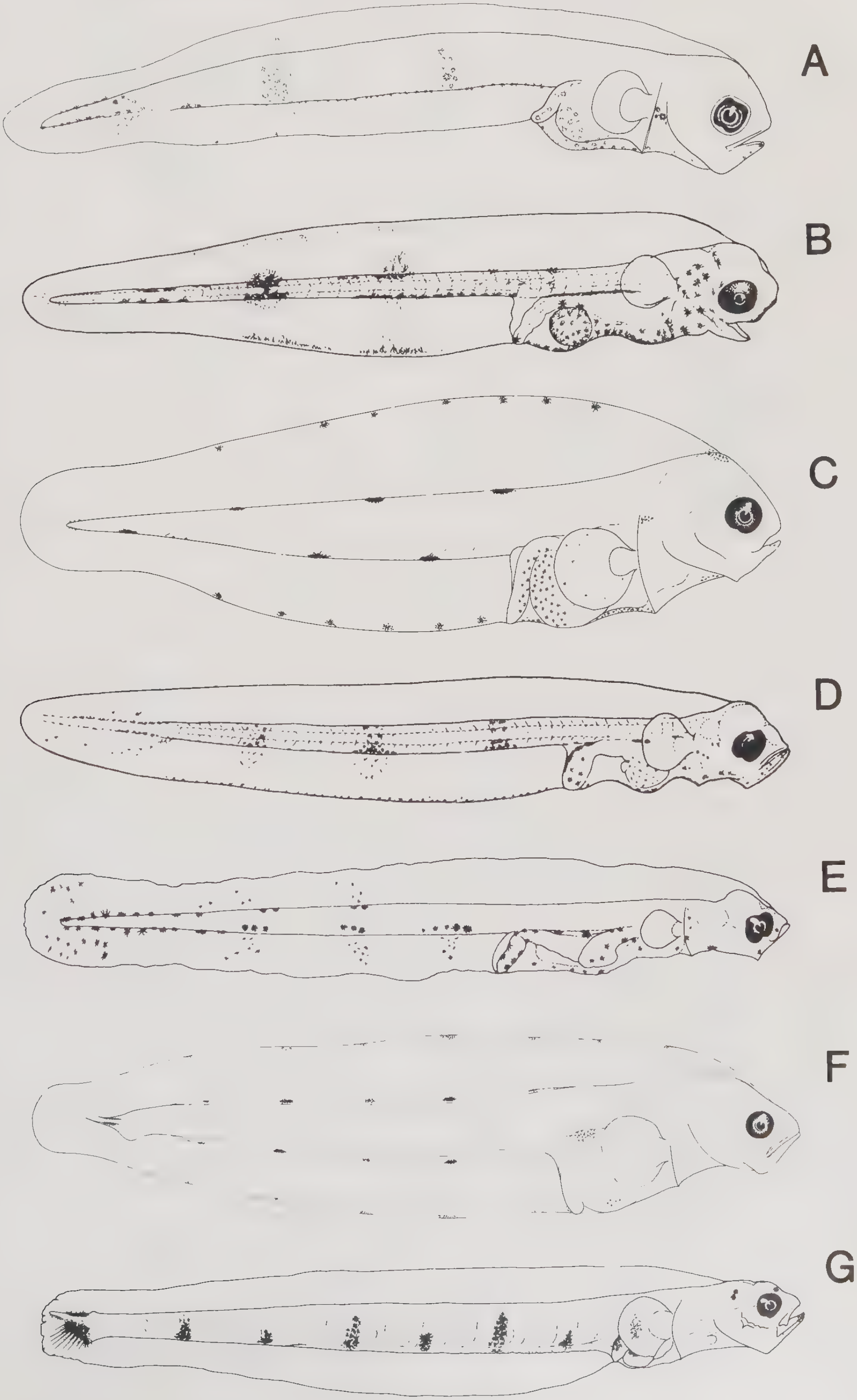
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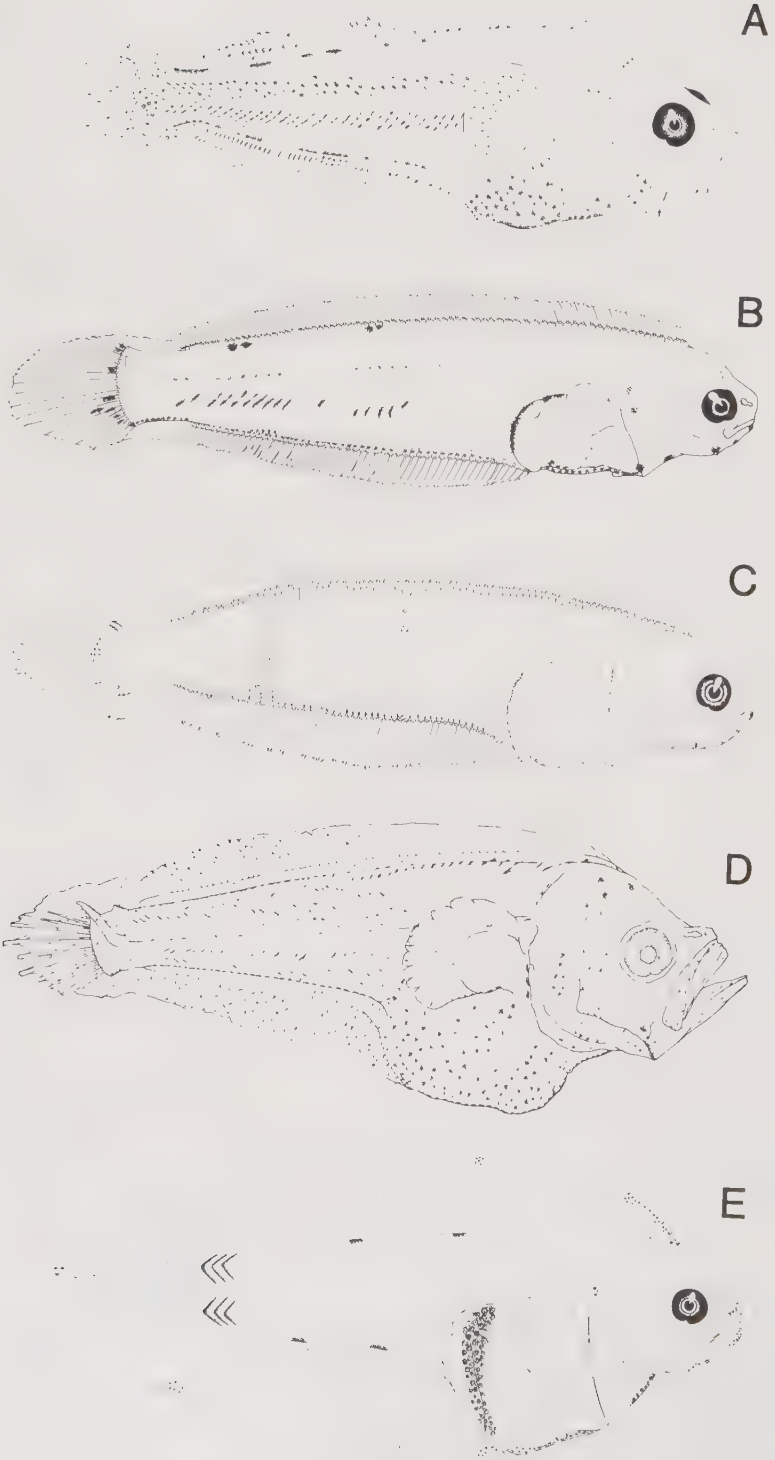
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TABLE 178. SIZE DATA AND NUMBER OF ELONGATE DORSAL RAYS FOR LARVAE OF SYMPHURINAE AND CYNOGLOSSINAE.

Taxon	Number of elongate dorsal rays	Size at hatching (mm)	Size at flexion (mm)	Size at transformation (mm)	References
Symphurinae					
Symphurus atricauda	5	1.9	9.4–10.8	19–24.2	Original
S. lacteus	4–5	—	6–<10	18	Kyle, 1913
S. ligulata	5	—	<10.5	32	Kyle, 1913
S. orientalis	5	—	>4.4–<9.3	>12.3	Pertseva-Ostroumova, 1965
S. plagiusa	4–5	<1.3	<6.2	<13	Hildebrand and Cable, 1930; Olney and Grant, 1976
Cynoglossinae					
Cynoglossus abbreviatus (as *Areliscus trigrammus*	2	3.2	—	—	Fujita and Takita, 1965
C. arel (as *C. oligolepis*)	2	—	—	—	Pertseva-Ostroumova, 1965
C. bilineatus	2	—	>4.0	6–8	Vijayaraghavan, 1957; Pertseva-Ostroumova, 1965
C. brevis	—	—	—	ca. 4.0	Balakrishnan and Devi, 1974
C. capensis	2–4	1.2	ca. 9.9	10–15	Brownell, 1979
C. cynoglossus	2	≤1.6	ca. 4.1	<4.7	Balakrishnan and Devi, 1974
C. kopsi (as *C. sibogae*)	2	—	7.6	—	Pertseva-Ostroumova, 1965
C. lida	2	<2.1	>4.6	—	Balakrishnan and Devi, 1974
C. lingua	—	—	—	17.7–?	Jones and Menon, 1951
C. macrostomus (as *C. semifasciatus*)	2	<2.5	4.2	ca. 5	Seshappa and Bhimachar, 1955
C. monopus	2	—	5–7	7.0	Balakrishnan, 1963
C. puncticeps	2	<1.4	ca. 4.2–?	ca. 4–5	Balakrishnan and Devi, 1974
C. robustus	2	1.85	—	—	Fujita and Uchida, 1957
C. semifasciatus	2	<2.0	7.2–11	11–12.5	Balakrishnan, 1961
Paraplagusia japonica	2	—	<10.2	ca. 12.2	Minami, 1982b

described several species from off west Africa. Life history series have been described for two achirine species of the western North Atlantic, *Trinectes maculatus* and *Achirus lineatus.* Eggs of achirines are smaller than in most soleines (Table 172) and, accordingly, size at hatching is also smaller; achirines and some soleines undergo notochord flexion and transformation at very small sizes (Table 177). Achirines are deep-bodied, with a large gut that occupies a major portion of the body volume, a large deep head with a distinct dorsal hump; eyes and jaws are large (Fig. 356). Preflexion larvae of *A. lineatus* develop spinous ridges above the eye (frontal bone), at the otic region (parietal and autopterotic bones) and on the preopercle. Also, five rows of papilla-like spines develop on the body. Larvae of *T. maculatus* develop bony ridges on the frontal, parietal and autopterotic bones. *A. lineatus* larvae are unique among described soleids in having an elongate third dorsal ray. Early larvae of *A. lineatus* are unpigmented but by late preflexion stage have developed pigment on the head, gut, elongate dorsal ray, dorsal and ventral body margins and blotches on the dorsal and anal fins. Early larvae of *T. maculatus* are heavily pigmented and have three large blotches in the dorsal finfold and two in the ventral finfold. In later larvae these blotches become dusky bars that overlie the nearly solid background pigment.

Soleines have a large head and jaws as in achirines but the eye is relatively smaller and the dorsal hump is less prominent (Fig. 356). Also, soleines are less deep-bodied and the gut occupies a relatively smaller portion of the body mass; in many soleine species the rounded gut mass protrudes well beyond the ventral profile. Pigmentation is highly varied ranging from species of *Aseraggodes* which lack pigment to species such as *Solea solea, Pegusa lascaris, Microchirus variegatus* and *Euryglossa pan* which are solidly covered with melanophores. A typical pattern appearing in many described species consists of a series of melanophores along the dorsum, ventrum and horizontal septum, and melanophores on the head, gas bladder and finfolds (Fig. 356).

Cynoglossidae (Fig. 357).—Two subfamilies, Symphurinae and Cynoglossinae, are recognized in the family. The first larval descriptions of the former are of *Symphurus lacteus, S. ligulata* and *S. pusilla* (Kyle, 1913). Hildebrand and Cable (1930) described a series as *S. plagiusa,* but Olney and Grant (1976) described a different series as *S. plagiusa* and pointed out that Hildebrand and Cable's descriptions must refer to another species. Pertseva-Ostroumova (1965) ascribed a larval series to *S. orientalis* and we have identified eggs and larvae of *S. atricauda.* Larval series or metamorphosing specimens have been ascribed to at least 11 types of cynoglossines; however, most of these are incomplete series and identifications are tentative (Table 178). Most cynoglossids are less than 2.5 mm at hatching;

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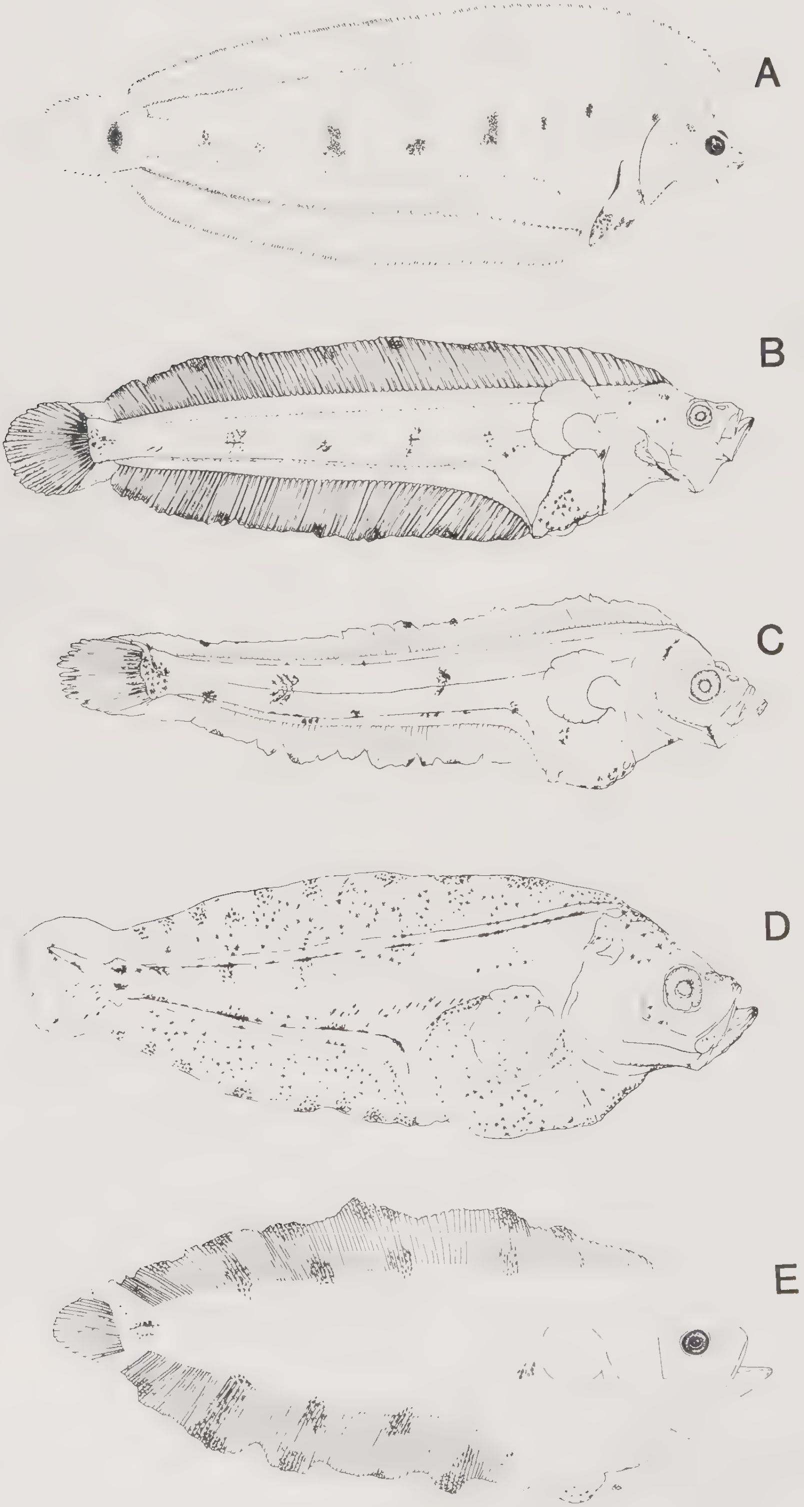
Fig. 353. Larvae of Pleuronectidae. (A) *Glyptocephalus zachirus,* 48.7 mm, redrawn from Ahlstrom and Moser, 1975; (B) *G. stelleri,* 24.6 mm, from Okiyama and Takahashi, 1976; (C) *Tanakius kitaharai,* 15.8 mm, ibid; (D) *Microstomus achne,* 8.8 mm, ibid; (E) *Embassichthys bathybius,* 16.2 mm, from Richardson, 1981b.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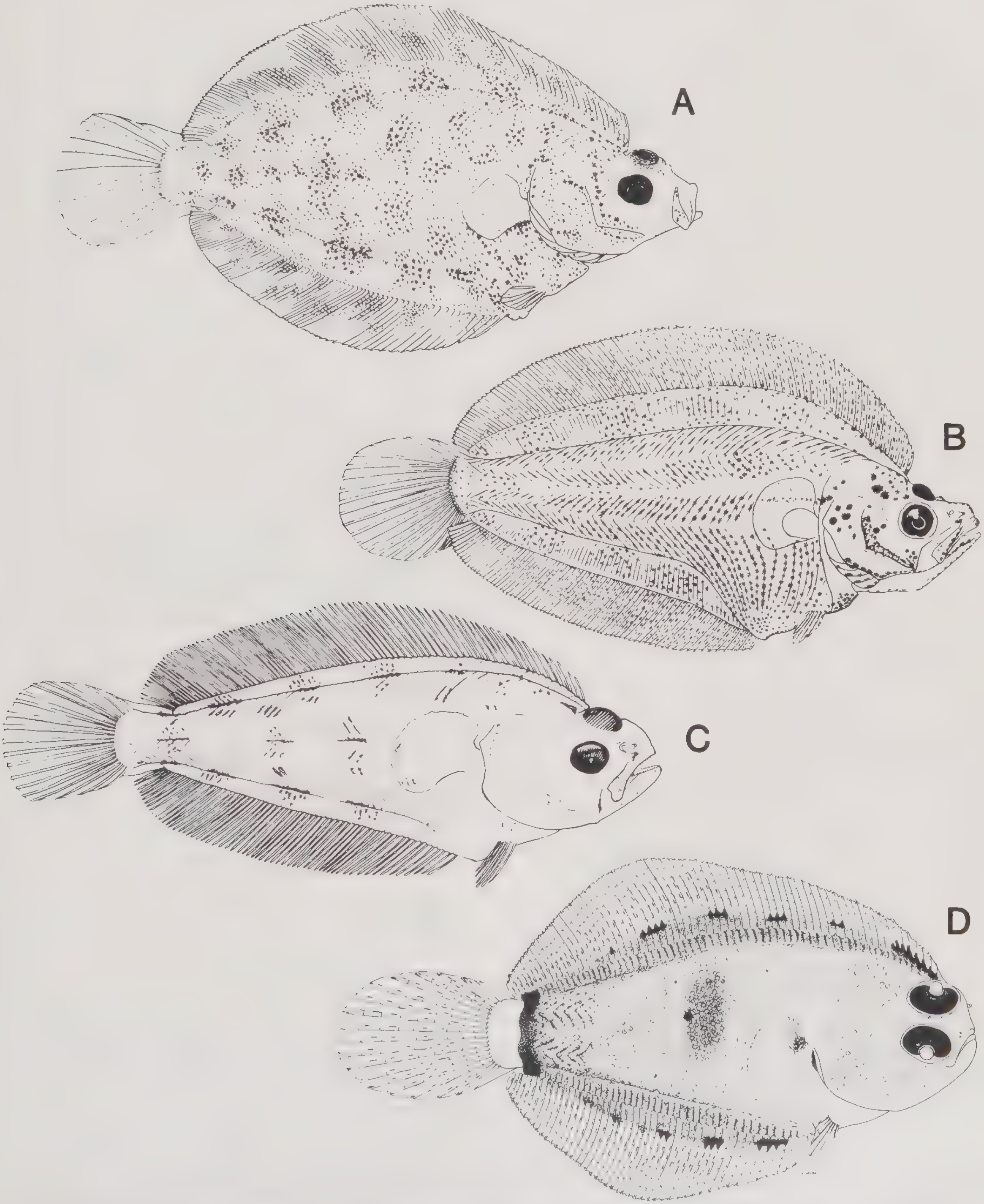

Fig. 354. Transforming specimens of Pleuronectidae. (A) *Hippoglossus stenolepis*, 24.0 mm, original; (B) *Eopsetta jordani*, 16.2 mm, CalCOFI 5104, Sta. 70.55; (C) *Lyopsetta exilis*, 22.0 mm, from Ahlstrom and Moser, 1975; (D) *Pleuronichthys ritteri*, 10.0 mm, from Sumida et al., 1979.

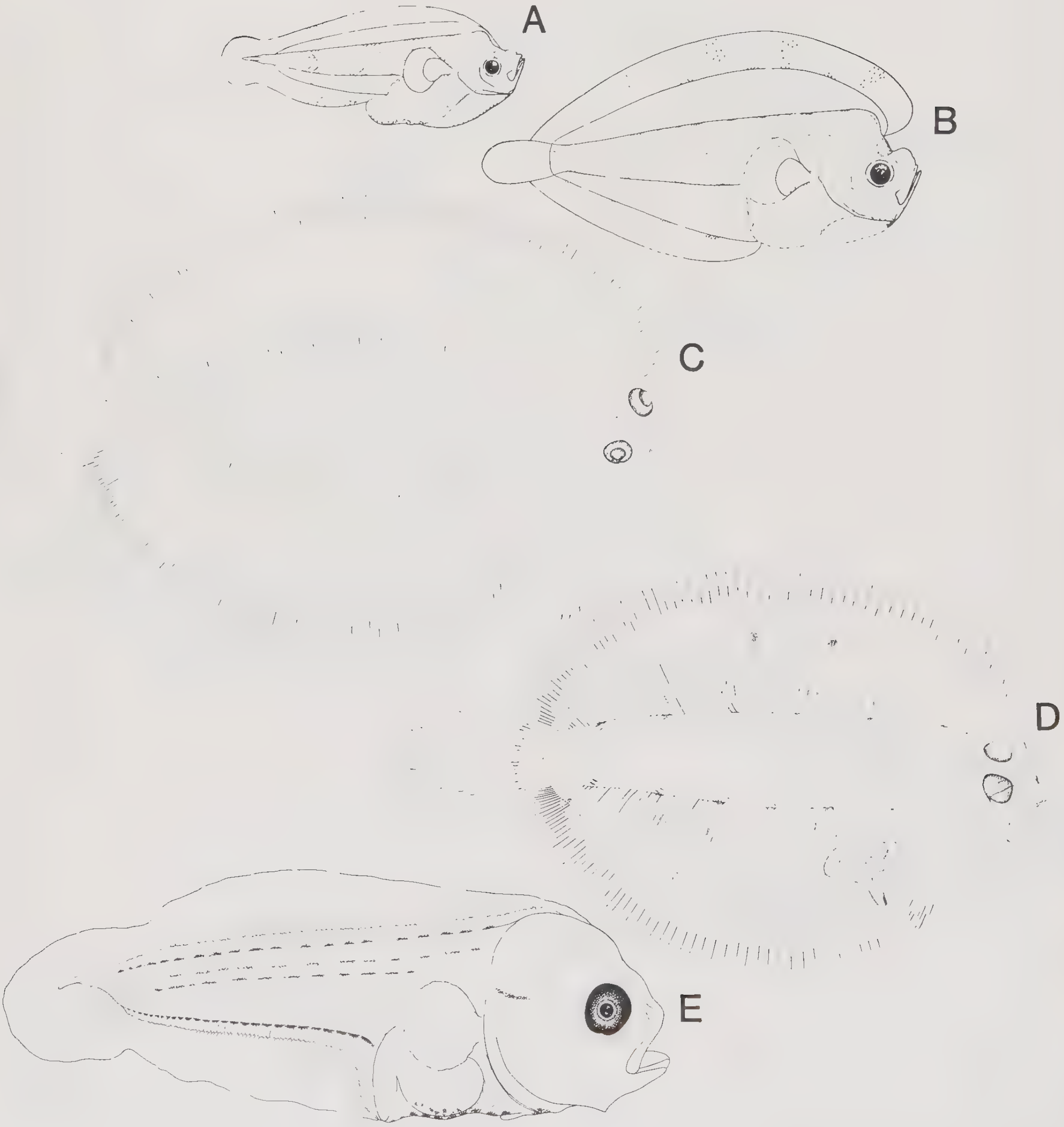

Fig. 355 Larvae and transforming specimens of Pleuronectidae. (A) *Samaris cristatus*, 6.4 mm, from Pertseva-Ostroumova, 1965; (B) *S. cristatus*, 8.7 mm, ibid; (C) *Samariscus* sp., ca. 24.0 mm; (D) *Poecilopsetta hawaiiensis*, ca. 29.0 mm; (E) *Pelotretis flavilatus*, 4.3 mm, redrawn from Rapson, 1940. C and D from P. Struhsaker, unpublished.

an exception is *C. abbreviatus* which has a relatively large egg. Notochord flexion and transformation occur at larger sizes in symphurines compared with cynoglossines and some *Symphurus* have an extended larval stage that exceeds 30 mm in length Table 178). Cynoglossid larvae are similar to those of soleids in having a large deep head and tapering body, but the jaws are relatively smaller in cynoglossids and the body is more attenuate (Fig. 357). The gut mass protrudes beyond the ventral profile and in some species it trails posteriad. In *S. lactea* a conical structure is attached to the trailing gut coil (Kyle, 1913). Cy-

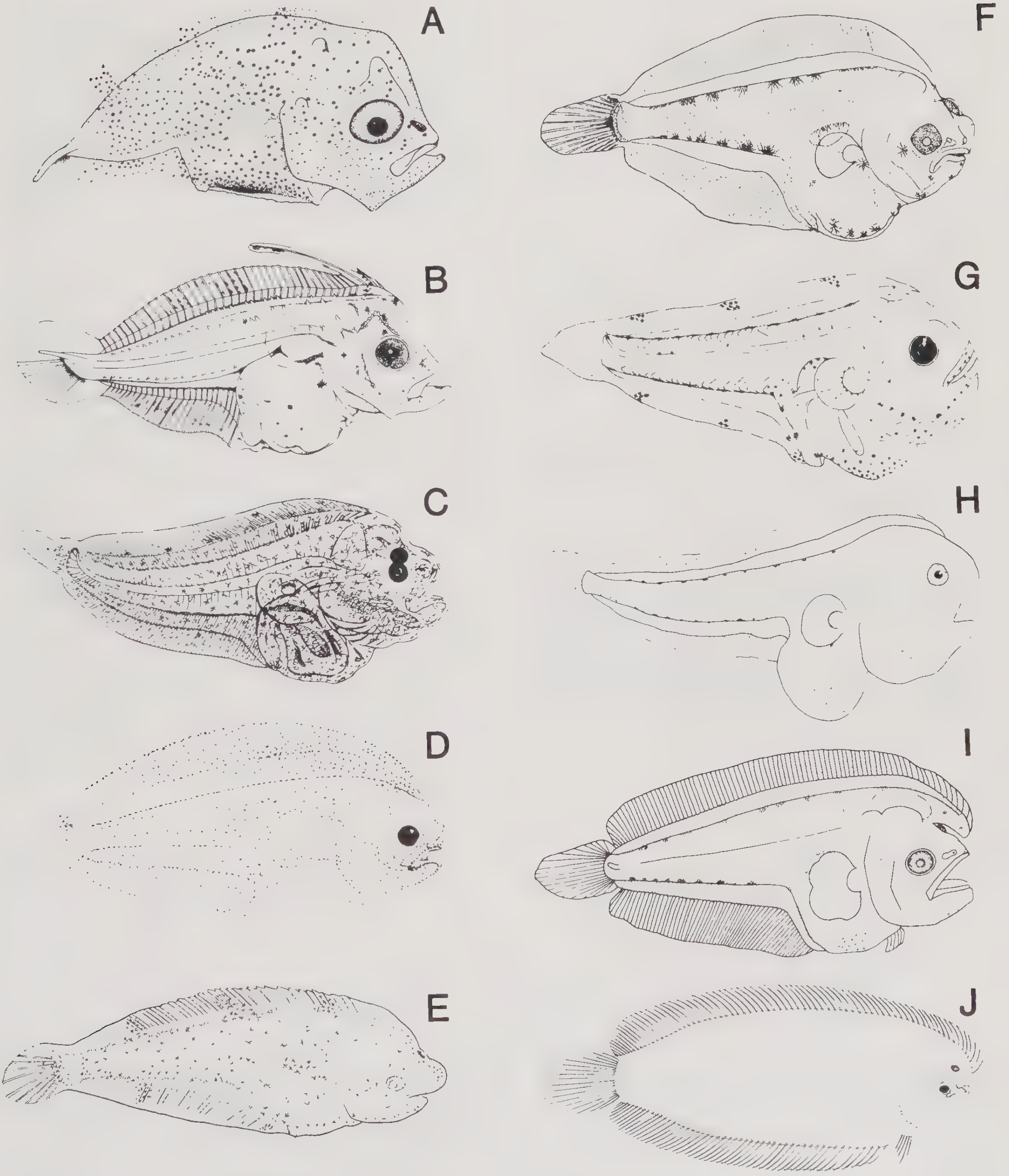

Fig. 356. Larvae and transforming specimens of Soleidae. (A) *Trinectes maculatus,* 2.0 mm, from Hildebrand and Cable, 1938; (B) *Achirus lineatus,* 3.1 mm, from Houde et al., 1970; (C) *Solea solea,* 7.5 mm, from Ehrenbaum, 1905–1909; (D) *Microchirus variegatus,* 10.0 mm, from Petersen, 1909; (E) *Euryglossa pan,* 4.6 mm, from Jones and Menon, 1951; (F) *Solea ovata,* 4.7 mm, from Jones and Pantulu, 1958; (G) *Microchirus ocellatus,* 5.1 mm, from Palomera and Rubies, 1977; (H) *Austroglossus microlepis,* 6.6 mm, from O'Toole, 1977; (I) *Heteromycteri japonicus,* 4.9 mm, from Minami, 1981b; (J) *Aseraggodes whitakeri,* ca. 27.0 mm, from P. Struhsaker, unpublished.

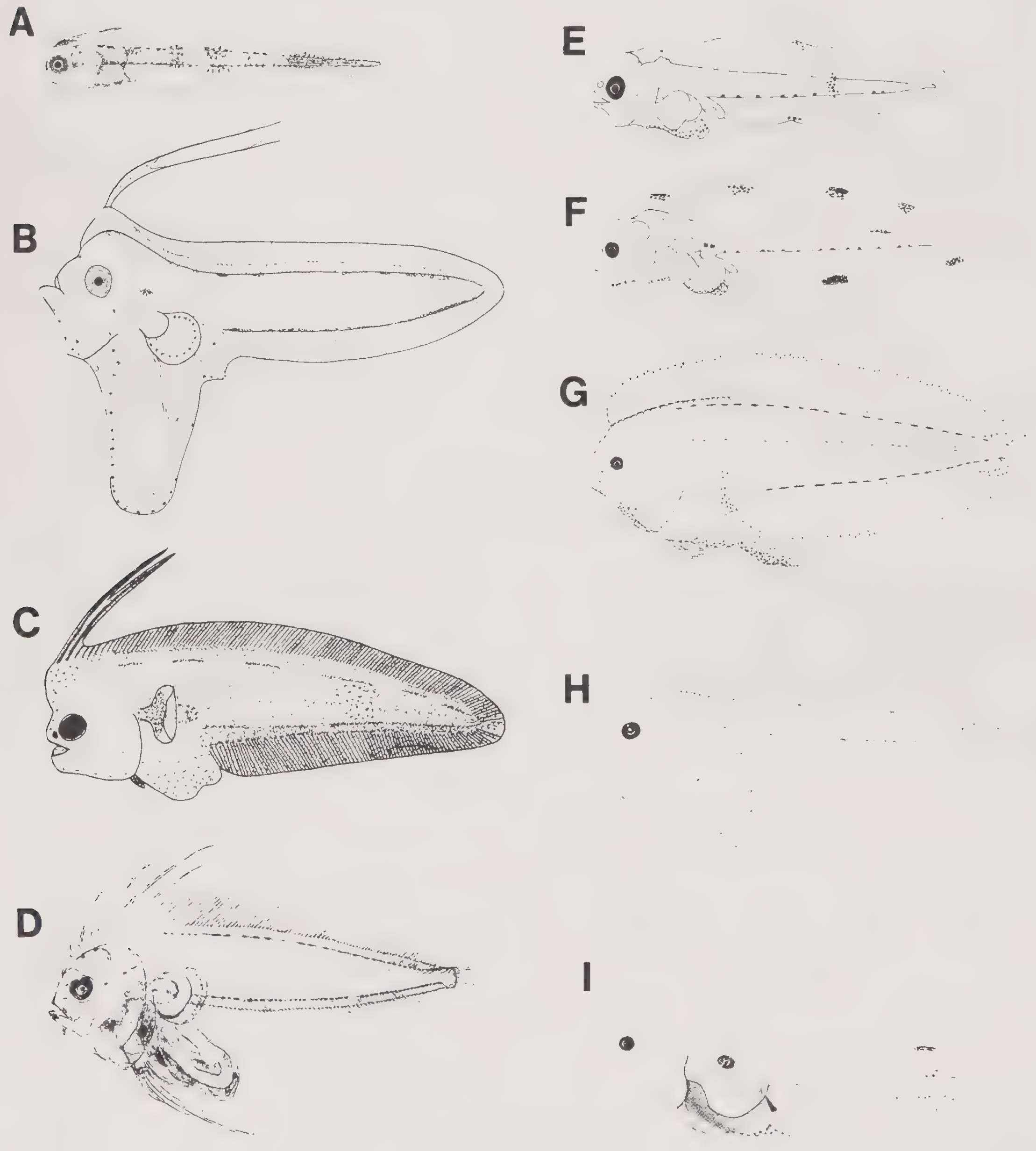

Fig. 357. Larvae of Cynoglossidae. (A) *Cynoglossus abbreviatus,* 5.0 mm, from Fujita and Takita, 1965; (B) *C. monopus,* 7.0 mm, from Balakrishnan, 1963; (C) *C. macrostomus,* 4.5 mm, from Seshappa and Bhimachar, 1955; (D) *Symphurus ligulata,* 10.5 mm, from Kyle, 1913; (E) *S. atricauda,* 4.0 mm, original, CalCOFI; (F) *S. atricauda,* 6.5 mm, original, CalCOFI; (G) *S. atricauda,* 12.8 mm, original, CalCOFI; (H) *S. plagiusa,* 6.2 mm, redrawn by Fahay (1983) from Olney and Grant, 1976; (I) *S. lactea,* 18.0 mm. from Padoa, 1956k.

noglossid larvae develop a crest consisting of elongate anterior dorsal rays, 2 rays in *Cynoglossus* and usually 4 or 5 in *Symphurus.* Pectoral fins are present during the larval period, but do not develop rays and disappear at metamorphosis. One species, *S. ligulata,* develops elongate third and fourth pelvic rays (Kyle, 1913; Padoa, 1956k).

Pigmentation in early larvae of *Cynoglossus* consists of 4–5 opposing blotches along the dorsum and ventrum, pigment on the head, gut and gas bladder. In some species, large blotches in the finfold distal to the dorsal and ventral midline blotches give the larvae a barred appearance. In later stages the midline blotches become more numerous and some species develop a series along the horizontal septum. Early larvae of *Symphurus* have small melanophores along the ventral midline, and in some species, also along the dorsal midline. Most species have a single bar posteriad on the tail and at least one, *S. atricauda,* has large blotches at the finfold margins. The head (particularly ventrally), gut, gas bladder and horizontal septum become pigmented and later-stage larvae have pigment patterns similar to *Cynoglossus* species.

Metamorphic stages

Pleuronectiforms undergo a remarkable metamorphosis during which one of the eyes, the left in dextral and the right in sinistral species, migrates around or through the head to a position dorsal to the non-migrating eye. Metamorphosis occurs over a wide size range among flatfishes, from about 5 mm in achirine soles (Houde et al., 1970) to greater than 120 mm in some bothines (Amaoka, 1971). Capture of specimens of the enormous flatfish larva observed by Barham (1966) from a diving saucer may double the maximum size for flatfish larvae. Most flatfishes metamorphose within the range of 10–25 mm (see preceding sections and Tables 173–178); the size interval over which the process occurs is smaller in species which metamorphose at a small size.

Metamorphosing specimens are relatively rare in plankton collections because 1) the process is transitory, 2) avoidance is increased at larger sizes, and 3) metamorphosing individuals may change habitat. Existing information indicates a variety of mechanisms of eye migration among flatfishes. In groups where the dorsal fin origin in larvae is at the posterior margin of the eye or more rearward (psettodids, citharids, scophthalmids, most paralichthyids, pleuronectids), a depression forms in the interocular region and the eye migrates over the dorsal midline anterior to the fin origin. Subsequently the dorsal fin extends forward to its adult position (except in psettodids). In larvae of bothids and the paralichthyid genera *Cyclopsetta, Syacium* and *Citharichthys* (some species), the dorsal fin is attached to the skull anterior to the eye and, during metamorphosis, the eye migrates through a slit which forms between the fin base and the skull. In some metamorphosing soleids the dorsal fin projects forward above the snout and the eye migrates through the space between this protuberance and the skull; subsequently the fin projection fuses to the skull (Houde et al., 1970; Palomera and Rubies, 1977; Minami, 1981b). Seshappa and Bhimachar (1955) described the process of eye migration in a captive specimen of *Cynoglossus macrostomus.* Just before eye migration a fleshy hook-shaped protuberance grew forward from the region of the head anterior to the dorsal fin origin. The right eye migrated through the space between the protuberance and the skull, after which the fleshy appendage fused to the dorsal region of the skull. The entire process took place over a 5-hour period during the night. A similar structure appears on advanced larvae of an unidentified cynoglossid illustrated by John (1951b) and this mechanism of eye migration may be widespread among cynoglossids.

During eye migration in flatfishes a number of other metamorphic events occur: 1) larval spines are lost, 2) elongate rays assume their juvenile proportions, 3) gut protrusions are brought into the body cavity and internal organs are rearranged, 4) gas bladder, if present, is lost, 5) pectoral fins develop rays, except in cynoglossids, some soleids, some bothids and *Mancopsetta,* where (one or both) fins are lost altogether during this period, 6) larval pigment patterns are replaced by juvenile patterns, 7) ossification of the vertebral column and other bony structures is completed, 8) intermuscular bones appear in bothids, and 9) scales form.

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Argentinoidei: Development and Relationships

E. H. Ahlstrom, H. G. Moser and D. M. Cohen

THE argentinoid fishes as here discussed have been considered a suborder by Cohen (1964b) and many other authors and a super-family of an expanded suborder that also includes the alepocephaloids by Greenwood and Rosen (1971). The latter group is not treated at length in this book, because little information on alepocephaloid ELH stages has appeared since Beebe's (1933a) survey which showed they hatch from large eggs and have direct development. The argentinoids *sensu strictu* appear to be monophyletic on the basis of four derived characters. One character concerns the development of rays in the finfold of the larva and is described later in this paper. A second character is the development of pustules on the inner surface of the chorion (not known for opisthoproctids). A third character relates to the swimbladder, which, when present, is served by a unique kind of rete mirabile, first described by Fange (1958) and further investigated by Marshall (1960) who named these structures micro-retia mirabilia. A fourth unique character, and one which never has been adequately studied and documented, is the tendency in the group for the vomer and palatines to assume the functions of the premaxillary and maxillary.

TABLE 38. LITERATURE REFERENCES FOR ONTOGENETIC STAGES OF ARGENTINOIDS.

Species	Egg	Larva	Transformation stage
Argentinidae			
Argentina elongata	Robertson, 1975a	—	—
A. silus	Schmidt, 1906c	Holt, 1898; Schmidt, 1906c	—
A. sphyraena	Sanzo, 1931d	Schmidt, 1906c; Sanzo, 1931d	Schmidt, 1906
Glossanodon leioglossus	Sanzo, 1931d	Schmidt, 1918; Sanzo, 1931d	Sanzo, 1931d
G. polli	—	—	Poll, 1953
G. semifasciatus	Nishimura, 1966	Nishimura, 1966	Nishimura, 1966
Microstoma microstoma	Sanzo, 1931d	Lo Bianco, 1903; Schmidt, 1918; Sanzo, 1931d	Schmidt, 1918
Nansenia groenlandica	—	Schmidt, 1918	Schmidt, 1918
N. oblita	Sanzo, 1931d	Schmidt, 1918; Sanzo, 1931d	Schmidt, 1918
Xenopthalmichthys danae	—	—	Bertelsen, 1958
Bathylagidae			
Bathylagus antarcticus	Yefremenko, 1982	Yefremenko, 1979a, 1983	—
B. euryops	—	Brauer, 1906; Tåning, 1931	Tåning, 1931
B. longirostris	—	Ehrenbaum, 1905–09; Murray and Hjort, 1912; Roule and Angel, 1930; Beebe, 1933b	Beebe, 1933b
B. nigrigenys	Pertseva-Ostroumova and Rass, 1973	Pertseva-Ostroumova and Rass, 1973	—
B. ochotensis	—	Ahlstrom, 1972b	Ahlstrom, 1972b
B. schmidti	Ahlstrom, 1969	Dunn, 1983a	Dunn, 1983a
B. stilbius	Ahlstrom, 1969	Ahlstrom, 1965, 1972b	—
B. wesethi	Ahlstrom, 1969	Ahlstrom, 1965, 1972b	—
Opisthoproctidae			
Bathylychnops exilis	—	—	Cohen, 1960
Dolichopteryx spp.	—	Roule and Angel, 1930	—
Dolichopteryx longipes	—	Beebe, 1933a	—
Macropinna microstoma	—	Chapman, 1939	—
Opisthoproctus grimaldii	—	Schmidt, 1918	—
Rhynchohyalus natalensis	—	Bertelsen et al., 1965	—
Winteria telescopa	—	Belyanina, 1982b	—

Although now there seems to be general agreement as to the genera to be included in the group, their internal arrangement is an unsettled matter. Opinions range from those of C. L. Hubbs (1953), who relegated all to a single family, to those of Chapman (1948 and papers cited therein), who advocated eight different families. Subsequently Cohen (1964b) classified the group in three families using inadequately evaluated characters.

Family Argentinidae (most genera are probably worldwide):
Subfamily Argentininae (benthopelagic, outer shelf to slope):
Argentina (12 species) and
Glossanodon (seven or more species).
Subfamily Microstomatinae (mesopelagic)[1]:
Microstoma (one or two species),
Nansenia (13 species) and
Xenophthalmichthys (one or two species).
Family Bathylagidae (meso-to bathypelagic):
Bathylagus (including *Leuroglossus* and *Therobromus*; about a dozen to 15 species; several species in the Arctic and Antarctic).
Family Opisthoproctidae (mesopelagic):
Group I:
Macropinna (one species; restricted to N. Pacific and eastern S. Pacific),
Opisthoproctus (two species),
Rhynchohyalus (one species; Atlantic and Indian Oceans) and *Winteria* (one species).
Group II:
Bathylychnops (one or more species), and
Dolichopteryx (perhaps half a dozen species).

An alternate arrangement presented by Greenwood and Rosen (1971) and essentially based on inadequately evaluated characters in the branchial arches and caudal fin skeleton proposed two families within a superfamily Argentinoidea: Family Argentinidae and Family Bathylagidae with Subfamily Bathylaginae (including Microstomatidae) and Subfamily Opisthoproctinae.

Unanswered questions concerning the systematics of the group are numerous and exist at all levels. Following is a summary. (1) What are the external relationships of the argentinoids? (2) How many distinct lineages exist within the group, how should they best be arranged with respect to each other, and how many families should be recognized? (3) Do *Argentina* and *Glossanodon* constitute a monophyletic group? If not, where does each belong? (4) How many genera should be recognized among the bathylagids? (5) Within the opisthoproct group do the elongate species in the *Bathylychnops-Dolichopteryx* group and the short-bodied species in the *Opisthoproctus* group constitute monophyletic lineages and if so should they be named? (6) Since species complements of genera are inadequately known, espe

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[1] Herein considered a distinct family.

TABLE 39. CHARACTERS OF THE EGGS OF ARGENTINOIDEI.

Species	Diameter	Number of oil globules	Distribution of oil globules	Diameter of oil globules	Source
Argentina sialis	1.31–1.66	1	vegetal pole	0.27–0.46	Original
Argentina silus	3.0–3.5	1	vegetal pole	0.95–1.16	Schmidt, 1906c
Argentina sphyraena					
(Mediterranean)	1.60–1.68	1	vegetal pole	0.44	Sanzo, 1931d
(North Sea)	1.70–1.85	1	vegetal pole	0.37–0.47	Schmidt, 1906c
Argentina elongata	1.67–1.80	1	vegetal pole	0.35–0.45	Robertson, 1975a
Glossanodon leioglossus	1.44–1.52	1	vegetal pole	0.36	Sanzo, 1931d
Glossanodon semifasciatus	1.5–1.6	1	vegetal pole	0.36	Nishimura, 1966
Microstoma microstoma					
(Atlantic)	1.60–1.72	1	vegetal pole	0.48–0.52	Sanzo, 1931d
(Pacific)	2.05–2.38	1	vegetal pole	0.49–0.82	Original
Nansenia candida	1.39–1.56	1	vegetal pole	0.41–0.49	Original
Nansenia crassa	1.05–1.30	1	vegetal pole	0.30–0.35	Original
Nansenia oblita	1.39–1.56	1	vegetal pole	0.40–0.53	Sanzo, 1931d
Bathylagus antarcticus	1.8–2.2	3–8	*	0.2–0.3	Yefremenko, 1982
Bathylagus schmidti	1.65–1.90	up to 9	*		Ahlstrom, 1969
Bathylagus stilbius	1.01–1.21	15–25	*		Ahlstrom, 1969
Bathylagus urotranus	1.03–1.21	15–25	*		Pertseva-Ostroumova and Rass, 1973, and original
Bathylagus ochotensis	0.92–1.1	many to two clumps	**		Original
Bathylagus wesethi	0.90–1.10	12–20	**		Ahlstrom, 1969
Bathylagus nigrigenys	0.83–1.09	12–20	**		Pertseva-Ostroumova and Rass, 1973, and original

* First grouped at vegetal pole, then move to beneath embryo, then coalesce to one at each equatorial pole.

** Numerous globules at vegetal pole then coalesce to one clump at each equatorial pole.

cially the mesopelagic ones, do presently available early life history specimens help define the species composition of argentinoid genera?

DEVELOPMENT

Eggs are known for 13 species of argentinoids and larvae for 22 species (Table 38). We present in this paper eggs of 5 additional argentinoid species and larvae of 8 additional species. These are: eggs and larvae of *Argentina sialis, Microstoma* sp., *Nansenia candida* and *N. crassa*; larvae only for *Bathylagus argyrogaster, B. bericoides, B. pacificus* and *Bathylychnops exilis*; eggs only for *Bathylagus ochotensis.*

Eggs

The eggs of argentinoids are pelagic, round, have a moderate to narrow perivitelline space, segmented yolk and a chorion with distinctive pustules on the inner surface (Table 39, Fig. 82). Egg diameters and oil globule characters are given in Table 39.

Argentinoid larvae hatch as relatively undifferentiated yolk-sac larvae, regardless of egg size. That is, yolk-sac larvae of *A. silus* at 7.5 mm, newly hatched from eggs 3.0–3.5 mm diameter, are at about the same stage of development as 3 mm bathylagid yolk-sac larvae which hatch from 1 mm eggs. In most marine fishes larger eggs produce more highly differentiated hatchlings.

Larvae

Body form.—Argentinid and bathylagid larvae are slender, those of microstomatids are deeper-bodied, and opisthoproctids have a wide variety of body shapes ranging from the slender larvae of *Bathylychnops* to the deep-bodied *Opisthoproctus* (Table 40, Figs. 83–87).

The gut is elongate and straight in argentinids and bathylagids, with the exception of *B. milleri* where the gut is straight but only about half the body length. In argentinids the gut is lined with transverse rugae for almost the entire length. In most bathylagids the gut has two distinct sections: an anterior section with longitudinal internal ridges, separated by a valve from a shorter posterior section with transverse rugae. The anterior section in *B. bericoides* and *B. longirostris* is markedly smaller in diameter compared with other species. Larvae of *B. wesethi, B. nigrigenys* and *B. argyrogaster* have transverse rugae along the entire length of the gut and the anterior section is relatively larger in diameter and thin-walled. Also the posterior section is subdivided by a second valve. *B. ochotensis* larvae develop a similar structure.

The gut in microstomatid larvae is long, but anteriorly has an elongate S-shaped fold that lies flat on the left side (Fig. 84). The lumen of the anterior folded section is characterized by longitudinal ridges whereas the posterior straight section has transverse rugae. The short pyloric section has longitudinal ridges. Schmidt (1918) shows the gut extended beyond the finfold margin in *Nansenia oblita* and trailing in early stage *Microstoma microstoma* larvae but we have not seen this in any specimens of these genera.

In opisthoproctids the gut is elongate in *Bathylychnops* and *Dolichopteryx* and relatively shorter in the deeper-bodied genera, *Macropinna, Rhyncholyalus* and *Opisthoproctus.* In all genera there is a sac-like stomach, which exits through a constricted pyloric section to the intestine. In *Bathylychnops* and *Dolichopteryx* the sac is elongate and pointed at its tip whereas in the other genera it is more rounded in form. The sac lies on the left side, except in *Bathylychnops* where it lies on the right. In the latter genus the pyloric constriction leads into a short but prominent bulbous section. *Dolichopteryx* is similar but lacks

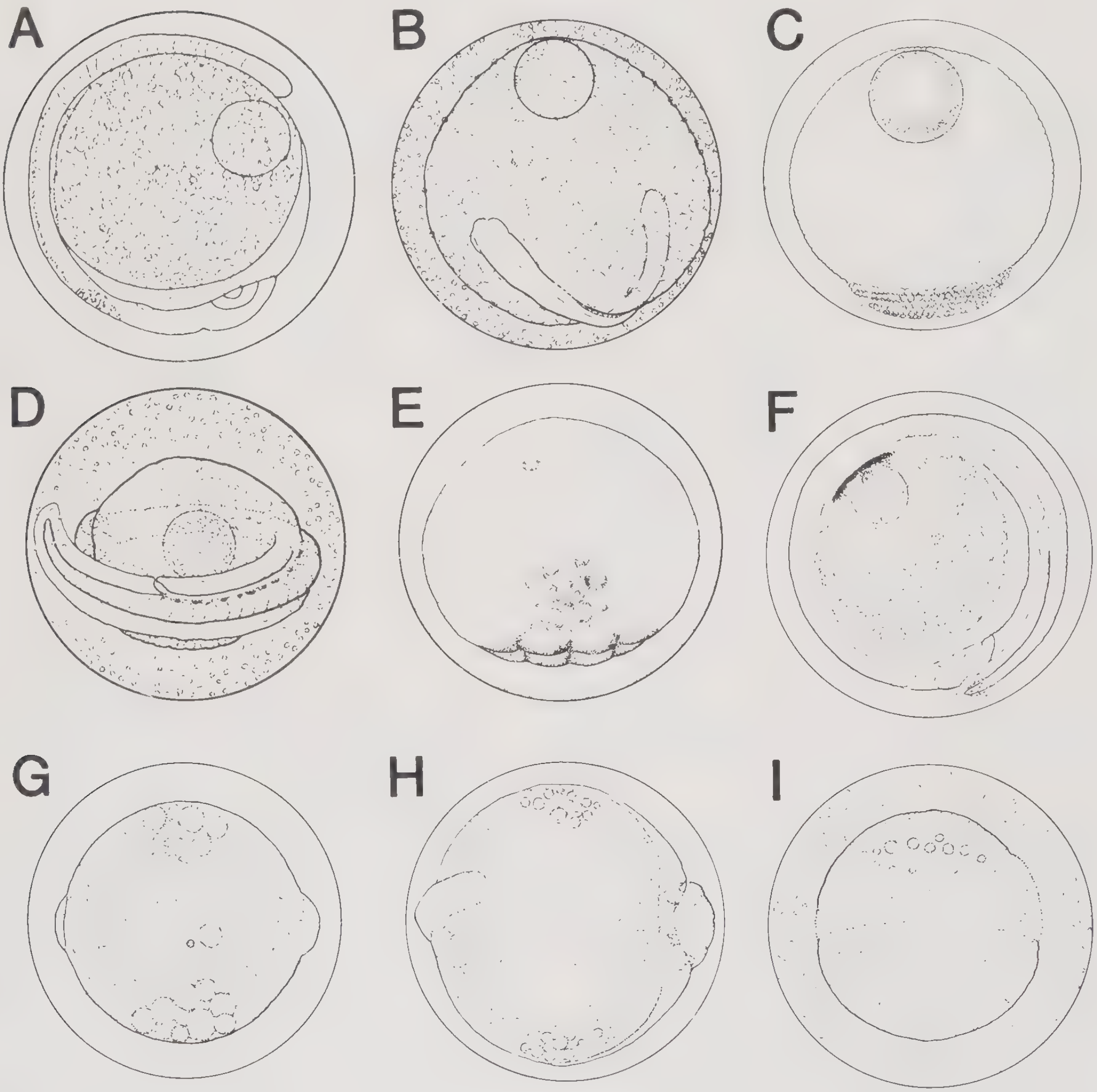

Fig. 82. Eggs of argentinoids. (A) *Argentina sialus,* 1.5 mm, CalCOFI 5103, Sta. 117.35; (B) *Microstoma* sp., 2.2 mm, CalCOFI 7511, Sta. 87.90; (C) *Nansenia candida,* 1.4 mm, CalCOFI Sta. 60.90; (D) *N. crassa,* 1.5 mm, CalCOFI; (E) *Bathylagus stilbius,* 1.1 mm, from Ahlstrom (1969); (F) *B. schmidti,* 1.8 mm, from Ahlstrom (1969); (G) *B. ochotensis,* 1.1 mm, CalCOFI 5002 Sta. 60.90; (H) *B. wesethi,* 1.0 mm, Ahlstrom (1969); (I) *B. nigrigenys,* 0.96 mm, CalCOFI 5106 Sta. 157.20.

the post-pyloric bulb. In *Macropinna* and *Opisthoproctus* there is a straight section leading posteriorly from the pylorus, which ends in an S-shaped fold and an enlarged rectal bulb, the latter described by Bertelsen and Munk (1964). The anterior section including the sac and pylorus have longitudinal internal ridges while sections posterior to this have transverse rugae. In late larval stages the entire section posterior to the pylorus becomes part of the S-shaped coil.

The head is relatively small in argentinids and has a rounded blunted anterior profile (Fig. 83, Table 40). It is slightly larger in most microstomatids, with the exception of *Microstoma* sp. (Pacific form) which has a small head. In most microstomatids the head has a rounded, blunted anterior profile and is bent slightly downward from the longitudinal axis. In both families the eye is either round or slightly ellipsoidal. In bathylagids the head is moderate in size but highly various in shape (Figs. 85, 86; Table 40). The snout is generally longer than in Argentinidae and Microstomatidae.

Eye shape and structure vary greatly within the bathylagids. *Bathylagus milleri* has a large, nearly round eye in contrast to

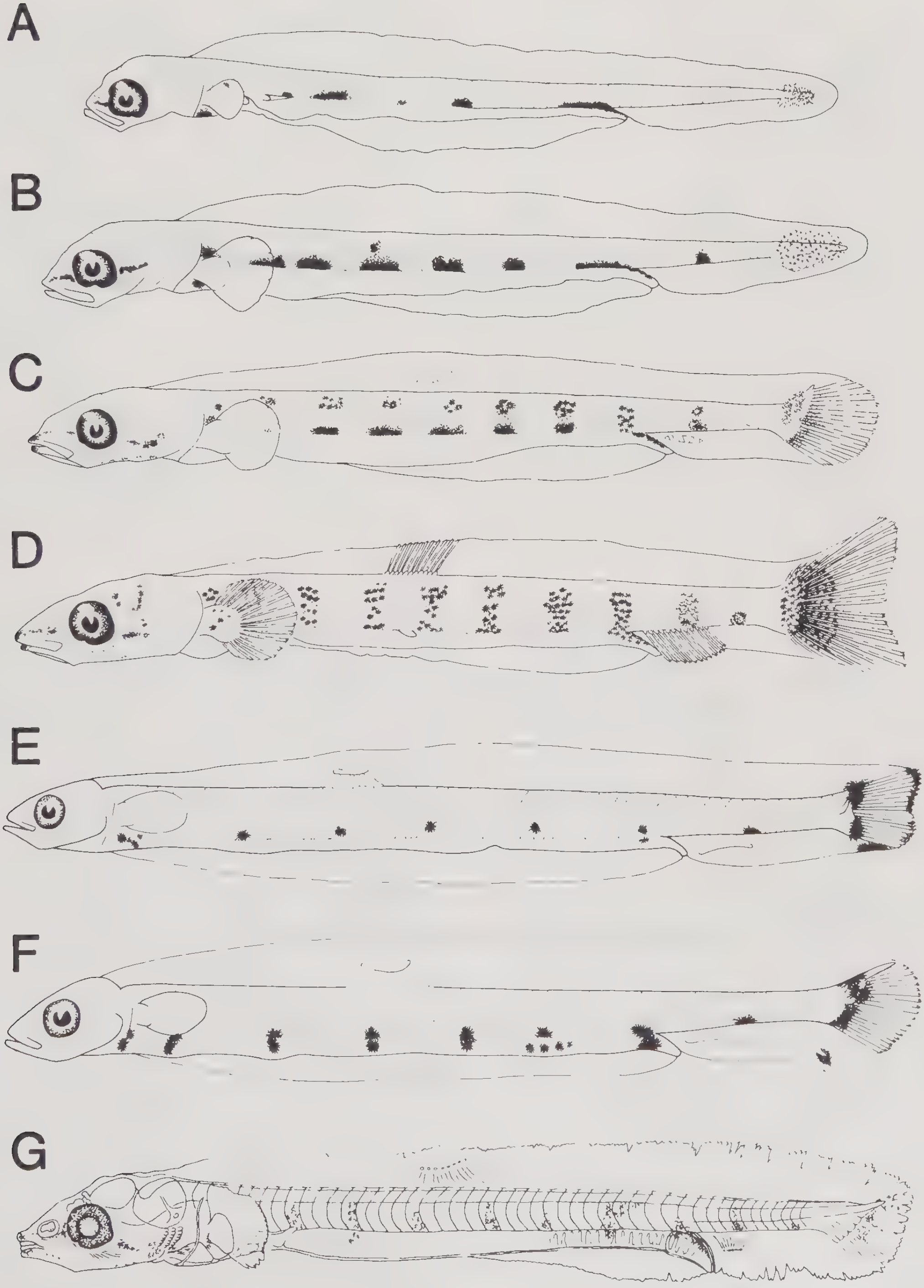

Fig. 83. Larvae of Argentinidae. (A) *Argentina sialis,* 7.0 mm, CalCOFI 5103 Sta. 117.35; (B) *A. sialis,* 9.0 mm, CalCOFI 5104 Sta. 97.40; (C) *A. sialis,* 17.5 mm, CalCOFI 5103 Sta. 120.35; (D) *A. sialis,* 21.0 mm, CalCOFI 5105 Sta. 123.40; (E) *A. silus,* 32.5 mm, redrawn from Schmidt (1906c); (F) *A. sphyraena,* 19.2 mm, ibid; (G) *Glossanodon semifasciatus,* 12.5 mm, from Nishimura (1966).

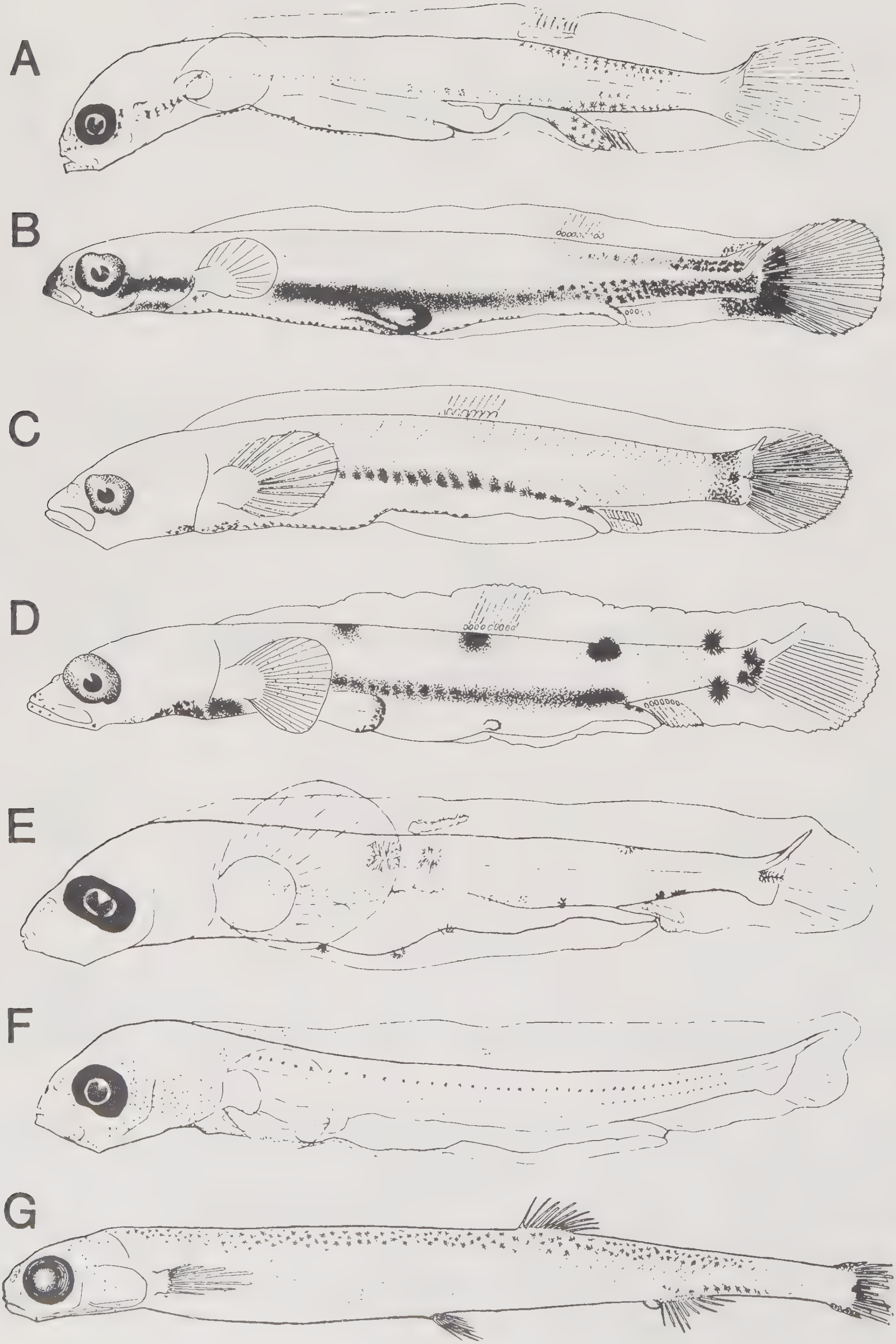
A
B
C
D
E
F
G

TABLE 40. COMPARATIVE MORPHOMETRY OF ARGENTINOID LARVAE. Mean values (%) of body proportions for three ontogenetic stages (preflexion-flexion-postflexion) are listed.

Species	Snout–anus distance	Head length	Head width	Eye length	Eye stalk length	Body depth	Snout–anal fin distance	Snout–dorsal fin distance	Snout–pelvic fin distance
	Body length	Body length	Head length	Head length	Head length	Body length	Body length	Body length	Body length
Argentina sialis	76-78-84	17-21-22	54-44-41	28-24-24	—	9-10-10	0-78-81	0-46-47	0-0-49
Microstoma microstoma	?-?-80	?-?-23	?-?-45	?-?-27	—	?-?-13	?-?-80	?-?-68	0-?-64
Microstoma sp. (Pacific)	76-79-80	17-19-19	53-49-44	31-29-27	—	8-10-10	0-78-81	0-70-72	0-64-67
Nansenia candida	74-77-82	21-25-26	60-50-44	36-28-28	—	12-14-16	0-75-82	0-54-58	0-56-61
Nansenia crassa	74-78-80	22-25-28	58-50-44	36-29-24	—	10-12-15	0-76-80	0-52-57	0-56-60
Nansenia groenlandica	?-78-80	?-27-25	?-50-42	?-21-23	—	?-15-15	?-77-80	?-52-52	?-54-57
Xenophthalmichthys danae	?-?-82	?-?-24	?-?-48	?-?-21	—	?-?-12	?-?-86	?-?-74	?-?-52
Bathylagus milleri	59-57-61	20-19-26	56-54-52	31-27-26	—	9-9-15	0-0-71	0-0-50	0-0-45
Bathylagus schmidti	72-76-78	16-19-22	50-52-46	39-26-25	.04-0-0	7-8-10	0-0-79	0-0-57	0-0-55
Bathylagus stilbius	74-77-80	20-22-24	54-53-47	32-25-20	.03-0-0	8-10-13	0-0-79	0-0-57	0-0-55
Bathylagus urotranus	78-82-81	20-24-28	56-53-46	27-18-21	.03-0-0	10-10-12	0-0-81	0-0-61	0-0-59
Bathylagus pacificus	76-85-81	22-24-25	39-42-44	29-22-18	28-29-20	8-10-13	0-81-80	0-49-48	0-51-51
Bathylagus euryops	78-80-82	18-20-20	46-50-50	31-26-25	10-7-3	10-11-12	0-78-80	0-45-48	0-0-47
Bathylagus bericoides	84-85-89	25-26-26	34-38-36	27-25-22	60-64-36	8-8-9	0-83-88	0-0-52	0-0-53
Bathylagus longirostris	85-88-92	26-27-25	34-34-34	24-20-19	54-48-27	8-10-10	0-88-90	0-0-53	0-0-57
Bathylagus ochotensis	81-85-90	20-23-23	44-44-44	32-21-21	17-15-15	8-10-11	0-83-87	0-53-54	0-56-56
Bathylagus wesethi	79-89-94	13-26-27	59-53-50	27-16-13	—	9-14-16	0-85-90	0-58-60	0-57-59
Bathylagus nigrigenys	80-86-93	20-29-28	78-60-53	30-18-14	—	12-16-18	0-86-90	0-57-60	0-0-60
Bathylychnops exilis	?-80-82	?-21-22	?-42-38	?-22-18	—	?-8-7	?-82-84	?-71-73	?-66-67
Dolichopteryx longipes	?-74-75	?-24-26	?-44-34	?-22-16	—	?-8-10	?-0-77	?-0-71	?-62-62
Macropinna microstoma	?-64-59	?-26-35	?-52-47	?-22-21	—	?-15-21	?-0-70	?-0-66	?-43-48
Opisthoproctus soleatus	?-?-80	?-?-37	?-?-46	?-?-18	—	?-?-18	?-?-83	?-?-63	?-?-40

other species which have relatively smaller, more elliptical eyes. Eyes are sessile in *B. milleri* and in the *B. wesethi* group but are stalked to some degree in all other species known. In *B. stilbius* and relatives (*B. urotranus,* and *B. schmidti*) the stalks are short and found only in early larvae. Stalks are longer and persist into later larval stages in other species, reaching a maximum of 65% of the head length in *B. bericoides.*

In opisthoproctids the head is moderate in size in the slender forms, *Bathylychnops* and *Dolichopteryx,* and longer and more massive, with a pronounced hump or bend at the nape, in the deep-bodied genera. All genera have an elongate snout and *Bathylychnops* has a unique triangular flap at its tip. *Bathylychnops* has round eyes that are rotated slightly dorsoanteriad. In the other genera, the eyes are tubular and directed dorsally, even in the smallest larvae available. Eye diverticulae with associated accessory retinae, characteristic of opisthoproctid adults, begin to form at the end of the larval period.

Fins.—A major feature of all argentinoid larvae is the development of a prominent median finfold in which the dorsal and anal fins develop, connected to the trunk by a series of hyaline strands (Figs. 83–87). The first fins to form are the pectorals. In argentinids and bathylagids they are relatively small and develop rays late in the larval period. Microstomatid and opisthoproctid pectoral fins are generally larger; however, there is a wide size range, from relatively small fins in *Microstoma* to large, fan-like fins in some species of *Nansenia* (e.g., *N. groenlandica*) to very elongate pectorals in *Dolichopteryx binocularis.* Ossification of rays begins earlier in these groups, usually before notochord flexion.

After the pectorals, the caudal fin is usually the next to form. In argentinids notochord flexion and development of principal caudal rays occurs at a size about midway in larval growth whereas in opisthoproctids this occurs earlier in the larval period. In bathylagids the process is somewhat delayed and in some species (e.g., *B. euryops, B. milleri*) notochord flexion may not be completed until near the end of the larval period.

The dorsal and anal fins begin to form at about the stage of notochord flexion in all argentinoids except opisthoproctids, where notochord flexion slightly precedes the appearance of dorsal and anal fins. The anal fin begins forming far posteriad in argentinoids, just posterior to the anus or the point of deflection of the free terminal gut section. In *B. milleri* and in the deep-bodied opisthoproctids with coiled guts there is a space between the anus and the anal fin origin.

The position of the dorsal fin is varied among argentinoids and forms in the larvae in approximately the same position that it will occupy in the adult. The fin has its most anteriad location in *Argentina* where its origin is well forward of the midpoint of the body (Fig. 83). The extreme case is found in *A. silus* where snout to dorsal origin is about 38% of the body length in larvae and about 43% in adults. In most bathylagids the dorsal origin is slightly anterior to mid-body. The exceptions are *B. stilbius* and relatives, where the dorsal origin is slightly posterior to mid-body, and *B. wesethi* and relatives where it is located still further posteriad.

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Fig. 84. Larvae of Microstomatidae. (A) *Microstoma microstoma,* 11.0 mm, from Schmidt (1918); (B) *Microstoma* sp., 12.0 mm, CalCOFI 5104 Sta. 90.52; (C) *Nansenia candida,* 8.4 mm, CalCOFI 5007 Sta. 100.70; (D) *N. crassa,* 8.5 mm, CalCOFI 5103 Sta. 137.50; (E) *N. groenlandica,* 10.0 mm, from Schmidt (1918); (F) *N. oblita,* 9.0 mm, ibid; (G) *Xenopthalmichthys danae,* 16.5 mm, from Bertelsen (1958).

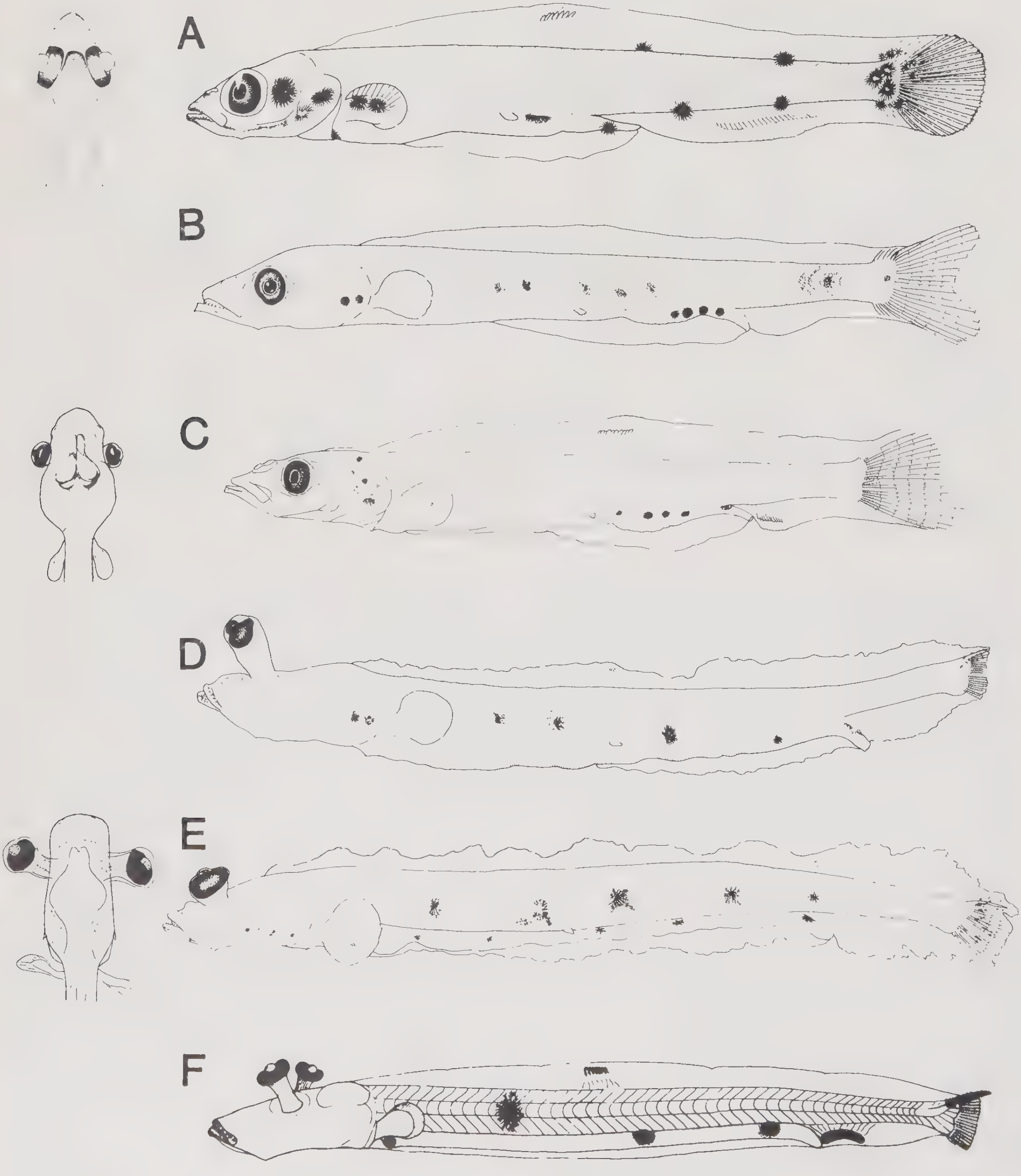


Fig. 85. Larvae of *Bathylagus*. (A) *B. milleri*, 27.5 mm, CalCOFI 5106 Sta. 70.60, dorsal view of 9.5 mm specimen at left; (B) *B. schmidti*, 31.5 mm, CalCOFI Northern Holiday Exped. Sta. 31; (C) *B. stilbius*, 23.2 mm, CalCOFI 4905 Sta. 111.38, dorsal view of 8.5 mm specimen at left; (D) *B. pacificus*, 21.4 mm, CalCOFI 7905 Sta. 63.60; (E) *B. euryops* 24.0 mm, dorsal view of 14.0 mm specimen at left, from Tåning (1931); (F) *B. antarcticus*, 26.5 mm, from Yefremenko (1983).

TABLE 41. MERISTICS OF ARGENTINOID FISHES.

Species	Vertebrae	Branchiostegal rays	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays	Procurrent caudal fin rays
Argentina							
aliceae	43–46	5	11–13	13–15	16–18	10–12	
australiae	50–53	5	10–12	12–13	13–14	11–13	
brucei	45–47	5	10–12	11–13	18–20	13–14	
elongata	52–55	5	10–12	11–14	13–16	11–12	
euchus	48–49	5	12	13–15	16–18	10–11	
georgei	48–51	5	10–12	10–13	16–19	12–14	
kagoshimae	51–52	5	10–12	11–13	15–17	11–12	
sialis	47–51	5	10–13	12–15	11–18	10–12	12+11
silus	65–70	6	11–13	11–17	15–18	12–13	
sphyraena	46–55	6	10–12	11–15	12–15	10–12	
stewarti	53–54	5	10–12	12–13	18–21	13–15	
striata	48–52	5	10–12	11–14	18–21	11–15	10+9
Glossanodon							
leiglossus	49–51	5	12–14	10–13	19–22	11–12	
lineatus		4	11–13	15	18–21	11–13	
mildredae	50–52	5	13	13	23	12–13	
polli		5	12–14	11–14	19–22	12–13	
pygmaeus	43–44	5	10–12	11–13	12–14	10–12	
semifasciatus	49	5	11–13	11–13	18–21	10–12	
struhsakeri	51–53		12–14	12–13	23–25	13–15	
Microstoma							
microstoma	45–47	3–4	11–12	8–9	8	9–11	11+11
sp. (Pacific)	49–50	4	9–11	7–8	11	9	10–11+10
Xenophthalmichthys							
danae		3	10–12	9–10	7	8–9	10+9
Nansenia							
atlantica	41–42	4	9–10	8–9	12–13	10–11	
ardesiaca	46–48	4	9–10	9–10	11–14	10–12	
candida	44–47	3	9–10	8–9	9–11	9–11	11+14
crassa	43–46	4	9–10	8–9	11–13	10–11	
groenlandica	42–45	3	9–10	8–10	11–13	10–12	
oblita	42–45	4	10–11	9–10	10–11	10–11	
Bathylagus							
antarcticus		2	9–11	21–25		9–10	
argyrogaster		2	12	14–15		8	
bericoides	48–53	2	10–11	18–22	10–12	9–10	
euryops	44–46	2	9–11	16–19	7–12	7–9	
greyae		2	11–13	13	12–13	10–11	
longirostris	48–51	2	10–12	19–21	9–12	9–10	
milleri	51–55	2	6–9	20–28	11–16	6–8	16–18+15–17
nigrigenys	41	2	11–12	14–17	10	8–10	
ochotensis	47–49	2	9–12	12–15	9–11	9–10	13–14+15–16
pacificus	45–49	2	8–9	15–22	7–11	7–10	13+13–14
schmidti	47–52	2	10–11	11–14	8–9	8–9	16–17+16
stilbius	38–42	2	9–11	11–14	8–11	8–10	12–16+13–15
urotranus	39–42	2	9–10	10–11	9–11	7–8	12–14+12–13
wesethi	43–46	2	12–13	14–16	10–11	9–11	14–15+14–15
Dolichopteryx							
anascopa		2	10	12	14	12	
binocularis		2	15	11	14	9	
brachyrhynchus		2	13	12	13	8	
longipes	41–44	2	10–11	8–9	13	8–9	
Bathylychnops							
exilis	81–84	2	14–16	13–14	12–13	7	
Rhynchohyalus							
natalensis		4	10–12	10	19–20	11–12	
Macropinna							
microstoma	36	3	11–12	14	17–19	10	
Winteria							
telescopa			8	8	12–14	9	

TABLE 41. CONTINUED.

Species	Vertebrae	Branchiostegal rays	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays	Procurrent caudal fin rays
Opisthoproctus							
grimaldii		2	12–14	8	11	10	
soleatus	31	2	10–12	13–14	9–11		

The dorsal fin forms in a variety of positions among microstomatids. In most species of *Nansenia*, the dorsal fin originates slightly posterior to mid-body, although in some species (e.g., *N. groenlandica*), its origin is slightly anterior to mid-body. The dorsal origin is further posteriad in *Microstoma*. In *M. microstoma* predorsal length is about 67–68% of the body length and assumes a more anterior position in adults (ca. 63%). In larvae of the Pacific species predorsal length is about 75% of the body length, and is slightly more posteriad in adults. In adult *Xenophthalmichthys* the dorsal origin is at mid-body; however, in the 16.5 mm specimen from the Atlantic (Bertelsen, 1958) predorsal length is 62% of the body length. In our single larva (12.2 mm) from the Pacific predorsal length is 75% of body length, indicating a marked anteriad migration during ontogeny or strong allometric growth posterior to the dorsal fin. Alternatively, the Pacific form may prove to be distinct when adult specimens are captured.

The dorsal fin in opisthoproctids is located posteriad on the body. This is most marked in the slender forms, *Bathylychnops* and *Dolichopteryx*, and reaches an extreme in *D. binocularis* where predorsal length is greater than ¾ of the body length. In the deep-bodied genera the dorsal origin is posterior to mid-body, but less so than in the slender-bodied forms.

The pelvic fins are the last fins to form in most argentinoids, usually late in the larval period. The exception is opisthoproctids where the pelvic fins form early in the larval period. In argentinids, bathylagids and microstomatids the pelvic fins form at about mid-body, below the dorsal fin. In the slender opisthoproctid genera the pelvics form well back on the body, but anterior to the dorsal fin. Among the deep-bodied genera, *Opisthoproctus* forms the pelvics far back on the body, beneath the dorsal fin. In *Rhynchohyalus* and *Macropinna* the pelvics develop just posterior to mid-body and anterior to the dorsal fin. In the larvae the fins are elevated to the sides of the body. This position persists in juvenile and adult *Macropinna* where the fins are located just behind and below the pectoral fin bases. The pelvic fins become elongate in *Dolichopteryx* and the deep-bodied genera. The pelvic fin base is pedunculate in opisthoproctid larvae, a condition that persists into the adults of some genera, notably *Dolichopteryx*. Argentinoids, except *Microstoma*, *Xenophthalmichthys* and some species of *Dolichopteryx*, develop adipose fins late in the larval period.

A summary of meristics of argentinoids is given in Table 41. The sequence of ossification of fins and other skeletal elements of *Bathylagus schmidti* is described by Dunn (1983a).

Pigmentation.—In argentinids, pigmentation consists of a series of 6–8 ventral trunk blotches that extend from the pectoral fin base to the end of the gut (Fig. 83). The series is continued posteriorly as 1 or 2 median ventral blotches and ends as a large blotch at the caudal region. The number of blotches is constant for each species, as is the sequence of formation. In *Argentina sialis* and *Glossanodon* the ventral blotches expand dorsally as lateral bars, but this does not occur in *A. silus* and *A. sphyraena*. These latter species differ additionally in lacking the internal head pigment which develops in *A. sialis* and *Glossanodon* larvae.

A feature common to most microstomatid larvae is a heavy line of embedded pigment above the gut (Fig. 84). In *Microstoma* this pigment continues forward to the gill arches and within the head anteriorly to the snout. In *Nansenia*, head pigmentation is superficial, or concentrated ventrally on the head. In *Microstoma*, an embedded dorsal line of pigment is located posterior to the dorsal fin. Dorsal pigmentation in *Nansenia* may take the form of a series of embedded blotches (e.g., *N. crassa*) or an embedded line of melanophores running the length of the body (e.g., *N. oblita*). Most microstomatids have conspicuous melanistic pigment associated with the caudal fin region. A notable feature of *Microstoma* and some *Nansenia* (e.g., *N. crassa*) is the presence of heavy melanistic pigment at the curve of the gut loop. Our single damaged specimen of *Xenophthalmichthys* (12.2 mm) has pigmentation similar to *Microstoma* but lacks the posterior dorsal body pigment and has a series of slanted melanophores along the hypaxial myosepta.

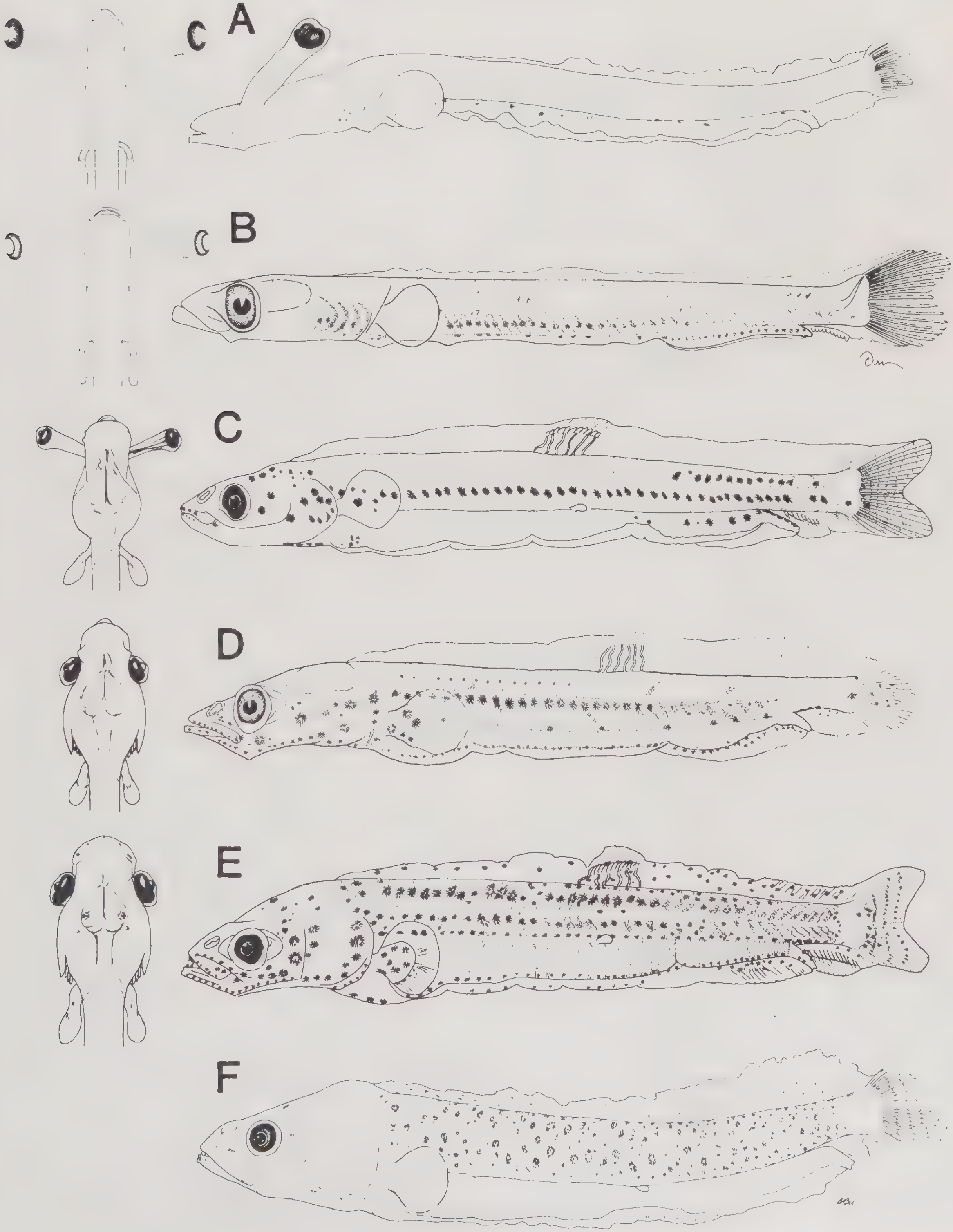
Pigment patterns in bathylagids may be grouped into two categories—those species with large isolated melanophores (Fig. 85) and those with linear series of smaller melanophores (Fig. 86). *Bathylagus milleri* has a unique pattern of opposing dorsal and ventral midline melanophores, large melanophores on the head and pectoral fin base and a large lateral blotch on the notochord tip.

Bathylagus stilbius and *B. urotranus* develop a series of 5–6 melanophores on each side of the posterior section of the gut. A single large melanophore, is found on the lower trunk midway between the pectoral fin and the anus and the head has melanophores, chiefly on the upper and lower jaws and opercle (Fig. 85). *B. schmidti* differs in having a series of lower trunk blotches and 1 or 2 postanal lateral blotches.

Bathylagus euryops has a series of 3–6 melanophores on the lateral surface of the gut and 3–5 large melanophores on the lateral surface of the trunk (Fig. 85). Other pigmentation consists

→

Fig. 86. Larvae of *Bathylagus*. (A) *B. bericoides*, 17.7 mm, Dana Sta. 4007, dorsal view of 11.8 mm specimen at left; (B) *B. longirostris*, 20.1 mm, SIO/STOW XIII Exped., dorsal view of 12.4 mm specimen at left; (C) *B. ochotensis*, 21.5 mm, CalCOFI 5106 Sta. 77.65, dorsal view of 8.5 mm specimen at left; (D) *B. wesethi*, 11.3 mm, from Ahlstrom (1972b), dorsal view of 8.5 mm specimen at left; (E) *B. nigrigenys*, 21.8 mm, SIO Shellback Exped. Sta. 92, dorsal view of 8.7 mm specimen at left; (F) *B. argyrogaster*, 17.1 mm, Dana Sta. 4003.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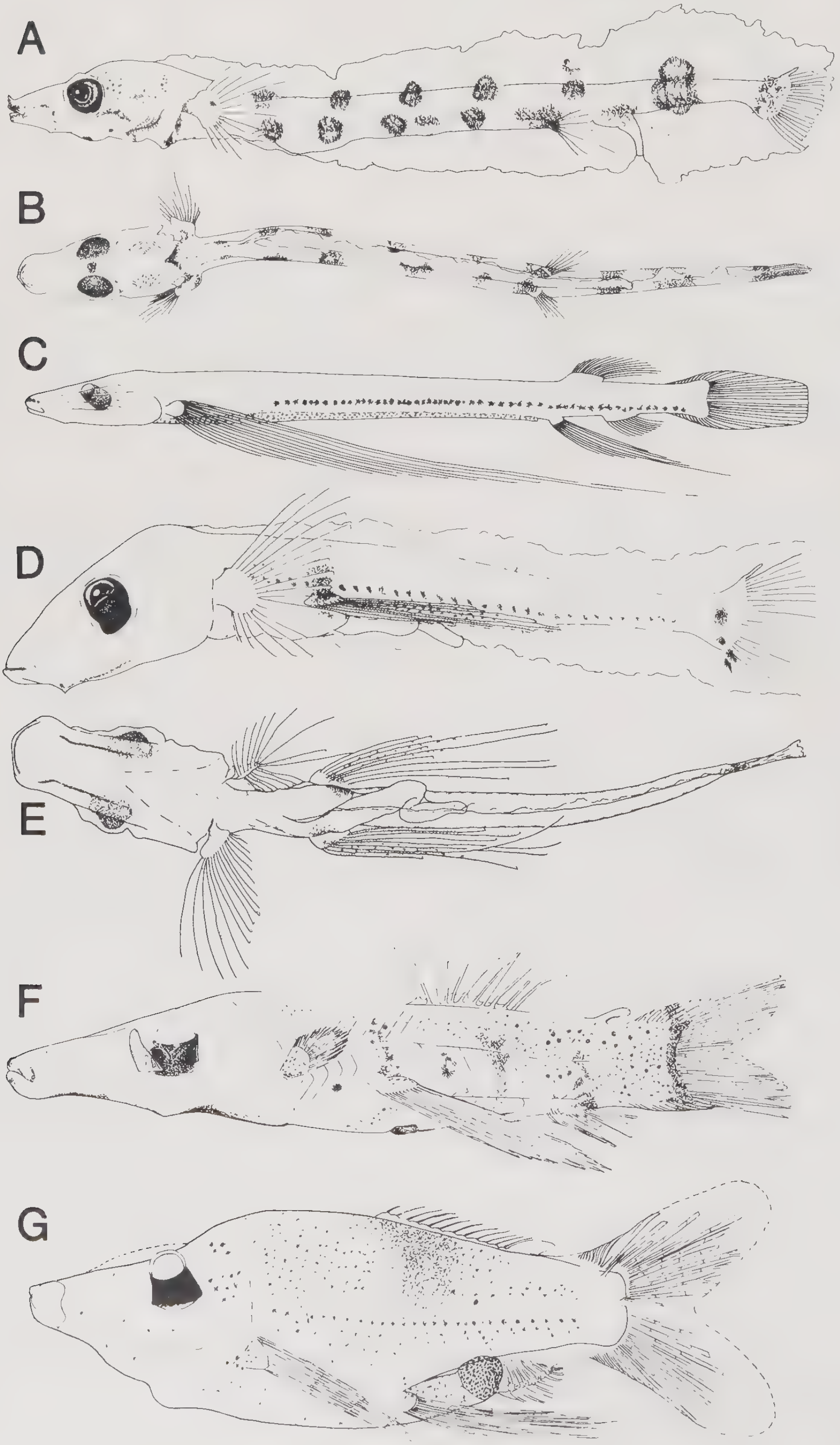
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Table 42. Characters used in Analysis of Four Argentinoid Groups.

Character number	Derived character state	Outgroup	Reference
1	Accessory cartilage at posterior tip ceratobr. 5	Osmerids	Greenwood and Rosen, 1971
2	$PU_1 + U_1$ fused	Teleosts in general	Goody, 1969
3	Light organs present	Teleosts in general	Bertelsen and Munk, 1964
4	Frontals fused	Teleosts in general	Cohen, 1964b
5	Epibr. 4 with one post. art. surface	Osmerids	Greenwood and Rosen, 1971
6	Larval gut with stomach	Osmerids	This paper, Hearne (this volume)
7	Pelvic fins form early and large	Osmerids	This paper, Hearne (this volume)
8	Swimbladder absent	Teleosts in general	Cohen, 1964b
9	Urodermal absent	Teleosts in general	Greenwood and Rosen, 1971
10	LL scales extend onto caudal fin	Teleosts in general	
11	Larval gut folded	Osmerids	Hearne (this volume)
12	Extrascapular attached to pterotic	Teleosts in general	Chapman, 1942
13	Uncinate process lacking on epibr. 4	Osmerids	Greenwood and Rosen, 1971
14	Pectoral fin forms early and large	Osmerids	This paper, Hearne (this volume)

of a line of small melanophores above and below the notochord tip, a patch of melanophores on the opercle and groups of small melanophores on the upper and lower jaws. *Bathylagus antarcticus* has 3 lateral gut spots, a large lateral trunk melanophore at the 10th–12th myomere, and head and notochord pigment similar to that of *B. euryops.* Early larvae of *B. pacificus* have a large lateral blotch at mid-body and another one posteriad on the body. Initially these melanophores are located at the junction of the gut and body but in later larvae are located on the trunk. Later a 3rd blotch forms midway between these two. A 4th lateral trunk blotch forms in some late larval specimens between the pectoral fin and the large mid-body blotch and melanophores form lateral to the liver and at the free terminal section of the gut. Head and notochord pigment is similar to *B. euryops* and *B. antarcticus.*

Bathylagus bericoides is unusual in having only a series of as many as 18 lateral gut melanophores (Fig. 86). Late postflexion larvae develop pigment on the lower jaw, isthmus, opercle, pectoral fin base and lateral caudal peduncle. *Bathylagus longirostris* develops a heavier pattern of pigmentation, beginning with a series of small melanophores on the posterior section of the gut in early larvae. Also in preflexion larvae a series of rectangular-shaped melanophores develops on the hypaxial myomeres. Later in the larval period the lateral gut series is extended forward along the entire gut, although with wider spacing than on the posterior gut section. Also, the epaxial myomeres develop rectangular-shaped melanophores, beginning posteriorly and accruing anteriorly. The head develops pigmentation from the opercle to the jaws (Fig. 86). *Bathylagus ochotensis* develops a similar pigment pattern except that the melanophores on the posterior gut section are comparatively larger and fewer, the anterior region of the gut lacks melanophores and the epaxial myomere series is limited to the posterior region.

Larvae of *B. wesethi, B. nigrigenys* and *B. argyrogaster* have a similar pigment pattern that differs markedly from that of other *Bathylagus* (Fig. 86). Initially there is a series of paired melanophores dorsolateral to the gut, extending from the pectoral fin base to the terminal section. These remain throughout the larval period but become embedded and obscured in late larvae. *Bathylagus nigrigenys* begins with about 8 pairs, which increase to 10, whereas *B. wesethi* begins with 6 pairs and has 7–8 during most of the larval period. Both species develop pigment at the notochord tip; *B. wesethi* has a dorsal and ventral spot, while *B. nigrigenys* has only a ventral spot. At notochord flexion a series of melanophores appears along the hypaxial region of the body and, soon after, a series develops along the epaxial myomeres. More lateral series are added and in late larvae the entire body is covered. Melanophores also form in the median finfold of advanced larvae. Initially head pigmentation consists of melanophores on the opercle and jaws but in later larvae the entire head is covered.

Opisthoproctid larvae have distinctive and, in some genera, heavy pigment patterns (Fig. 87). *Bathylychnops* has a dorsal series of 6 large paired blotches that permeate the musculature, bridge across the longitudinal septum and expand onto the finfold. A series of 8 large ventrolateral blotches alternate with those of the dorsal series, with the exception that the postanal blotch lies opposite the dorsal blotch and expands to form a band. A large blotch covers the base of the caudal fin. The head is heavily pigmented with superficial melanophores on the branchiostegals, urohyal and lateral brain and deeply embedded melanophores in the snout, jaws, cheek and ventral brain region. The lower limbs of the gill arches and their filaments are heavily pigmented as are both the pectoral and pelvic fin bases.

The species of *Dolichopteryx* have lateral series of melanophores above the gut and some species develop serial melanophores on the hypaxial myomeres (Fig. 87). Head pigment consists of melanophores on the jaws, gill arches and, in most species, the internal snout region. *Macropinna* develops a series of slanted melanophores, one on each hypaxial myomere, and a heavy embedded blotch at the pelvic fin base, that expands both dorsad and ventrad as a band. The caudal fin base has a large blotch

Fig. 87. Larvae of Opisthoproctidae. (A) *Bathylychnops exilis,* 15.6 mm, CalCOFI 7203 Sta. 67.80; (B) Ventral view of above; (C) *Dolichopteryx binocularis,* 58.0 mm, redrawn from Roule and Angel (1930); (D) *Macropinna microstoma,* 11.7 mm, CalCOFI 7412 Sta. 120.50; (E) Ventral view of above; (F) *Rhynchohyalus natalensis,* 23.0 mm, from Bertelsen et al. (1965); (G) *Opisthoproctus grimaldii,* 14.0 mm from Schmidt (1918).

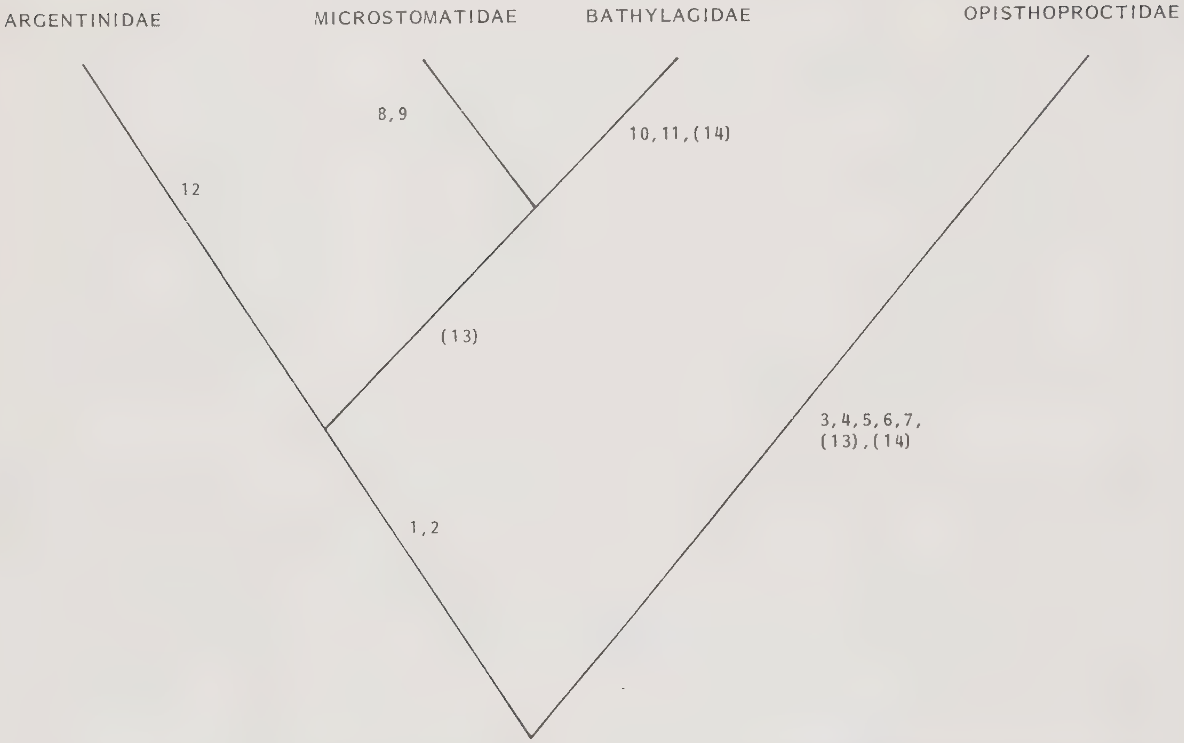

Fig. 88. Cladogram showing the distribution of character states in four nominal families of argentinoid fishes. Numbers refer to characters in Tables 42 and 43. Parentheses indicate character reversals.

and in the gut region there is pigment above the terminal section and ventral to the liver. Head pigment is confined to the lower jaw. The pigment pattern of *Rhynchohyalus* as described by Bertelsen et al. (1965) consists of a series of four dusky bars beginning at the pelvic fin and ending at the caudal fin base. Embedded beneath these is a layer of diffuse melanophores which becomes denser toward the caudal. The pectoral fin bases are pigmented and in the ventral region there are melanophores on the isthmus and gut. The anal light organ is covered with a melanistic sheath. The late larval specimen of *Opisthoproctus grimaldii* illustrated by Schmidt (1918) shows a diffuse covering of melanophores over the body and a dusky bar extending down from the dorsal fin. A 10 mm larva of *O. soleatus* in our collection has a pigment pattern similar to *Macropinna,* with a series of slanted melanophores on the hypaxial myomeres, embedded blotches at the pelvic and caudal fin bases, pigment at the liver and ventrally at the angles of the lower jaw.

Transformation stage

In argentinids transformation from larva to demersal juvenile is a prolonged process and pelagic juveniles with the retained larval pigment blotches or bars have been reported many times (see Cohen, 1958; Nishimura, 1966). Morphological changes (e.g., deepening of the body, prolongation of the snout, eye enlargement) and the masking of the larval pigment occur gradually. The beginning of this stage may be defined by the folding of the anterior gut region to form a stomach. This occurs at 25–30 mm in *Argentina sialis,* but has not been documented for other species. Pelagic juveniles of *Glossanodon* and *A. sialis* develop a silvery stripe at the lateral line region. This has not been reported for pelagic juveniles of *A. silus* and *A. sphyraena* and may afford an additional character for separating *Argentina* into two groups. The end of the pelagic juvenile stage, marked by the development of scales and silvery integument, is attained

Table 43. Distribution of Character States in Four Nominal Families of Argentinoid Fishes. Direction of transformation A → B.

Character number	Argentinidae	Micrstomatidae	Bathylagidae	Opistho-proctidae
1	B	B	B	A
2	B	B	B	A
3	A	A	A	B
4	A	A	A	B
5	A	A	A	B
6	A	A	A	B
7	A	A	A	B
8	A	A	B	A
9	A	A	B	A
10	A	B	A	A
11	A	B	A	A
12	B	A	A	A
13	A	B	B	B
14	A	B	A	B

at various lengths by different species. Schmidt (1906c) reports complete transformation at about 50 mm in *A. sphyraena* and at a much larger size in *A. silus.* Size at completion of transformation in *Glossanodon* species is also in the 50–100 mm size range (Nishimura, 1966).

Microstomatids develop a lustrous guanine layer on the integument in late larvae and some species develop distinct juvenile pigmentation. In *Microstoma* juveniles the region of the body from the dorsal fin origin posteriad is more darkly pigmented than the rest of the body, and grades to a solid black pigment at the caudal fin base. Juveniles of some *Nansenia* species develop heavy melanistic pigment at the base of the caudal fin and often at the base of the adipose fin (Schmidt, 1918; Kawaguchi and Butler, in press).

Bathylagids have a direct transformation and undergo a marked morphological change from the slender larval form to the juvenile form, characterized by a large head and eyes and deeper body. The gut becomes coiled and covered by a black peritoneal sheath. The head becomes heavily pigmented but the body is slower to develop the black pigment characteristic of all *Bathylagus* species (other than the *B. stilbius* group) and, in species such as *B. euryops* and *B. milleri,* the large larval melanophores are visible in specimens up to 30 mm and 50 mm respectively.

In the deep-bodied opisthoproctid genera transformation to the juvenile stage is marked by deepening of the body and attainment of melanistic integument and large scales. Cohen (1960) described the large (up to 124 mm) transitional specimens of *Bathylychnops* which are semi-transparent and retain the large larval pigment blotches. Sexually mature specimens of *Dolichopteryx* are semi-transparent, have a membranous body envelope, poorly developed musculature, an exposed gut covered only by peritoneum, weakly attached fins and melanistic pigment of the type usually associated with larvae (Cohen, 1960).

Relationships

Our survey of argentinoid ontogenetic characters provides insight into some of the systematic questions posed at the beginning of the paper. A close relationship between argentinoids and alepocephaloids is not supported since the latter hatch from large eggs (estimated at 3–4 mm based on size of yolk-sac larvae), have direct development, and share no specialized ontogenetic characters with argentinoids. Four major argentinoid lineages can be defined by specializations of the eggs and larvae and thus four families recognized: Argentinidae, Microstomatidae, Bathylagidae, and Opisthoproctidae. *Argentina* and *Glossanodon* have generalized larvae except that all known species have distinct lateral series of melanistic blotches or bands, not found elsewhere among argentinoids. The pattern of banding does not separate the two genera.

All known bathylagid eggs have multiple oil globules. A number of bathylagid groups are apparent from larval characters: 1) *milleri,* 2) *stilbius-schmidti-urotranus,* 3) *euryops-pacificus-antarcticus,* 4) *bericoides-longirostris,* 5) *wesethi-argyrogaster-nigrigenys.* Of these groups, *stilbius-schmidti-urotranus* has the most generalized morphology and pigmentation, lending no support for its separation as a distinct genus.

Opisthoproctid larvae share a number of neotenic features, including a saccular stomach. Except for body shape, *Dolichopteryx* shares more derived larval characters with the deep-bodied genera than with *Bathylychnops,* and the latter has a number of characters unique to opisthoproctids. Division of the family based on body shape is not supported by ontogenetic evidence.

Ontogeny offers little information on species composition of genera, because only a fraction of argentinoid eggs and larvae are known. However, egg and larval characters clearly separate Atlantic and Pacific *Microstoma* as distinct species. *Bathylagus bericoides* larvae from the Atlantic and Pacific are indistinguishable. The same is true for *B. longirostris* from all oceans. *Bathylagus nigrigenys* and *B. argyrogaster* larvae are indistinguishable, lending support for a single circumtropical species. *Bathylagus stilbius* eggs and larvae are indistinguishable from those of *B. urotranus.*

We have attempted to analyze the distribution among four nominal groups of argentinoids, of 14 characters, four of which are taken from developmental stages and 10 from the adult (Table 42). We have used teleosts in general and osmerids as our outgroup following Fink and Weitzman (1982). Distribution of character states are presented in Table 43.

A possible arrangement of groups based on the fewest number of character reversals is presented in Figure 88. Opisthoproctidae appears to be a well-founded family. More precise interpretation of the inter-relationships and nomenclatural ranking for argentinids, microstomatids, and bathylagids requires additional data.

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Families Gonostomatidae, Sternoptychidae, and Associated Stomiiform Groups: Development and Relationships

E. H. Ahlstrom, W. J. Richards and S. H. Weitzman

A summary of known information about the larvae and relationships of the stomiiforms with elongate gill rakers in adults was published by Ahlstrom (1974). The present paper is an addendum to that contribution and includes additional information, both published and unpublished, gleaned from early life history stages and from adults. We also append some tentative new hypotheses of relationships within this "group" of stomiiforms.

TABLE 47. SUMMARY OF DIAGNOSTIC CHARACTERS FOR EGGS OF CERTAIN STOMIIFORM FISHES.

Species	Egg diameter	Oil globule	Diameter	Yolk	Special features	Illustrated	Source
Argyropelecus hemigymnus	0.92–1.04	1	0.26–0.28	segmented	large oil globule	Yes	Sanzo, 1928
Ichthyococcus ovatus	0.80	1	0.24	segmented	large oil globule	Yes	Sanzo, 1930b
Maurolicus muelleri	1.63	1	0.25	segmented	hexagonal pattern on shell	Yes	Mito, 1961a
	1.32–1.58	1	0.26–0.28	segmented		Yes	Sanzo, 1931d
Vinciguerria lucetia	0.58–0.74	none		irregularly segmented	thin inner shell membrane	Yes	Ahlstrom and Counts, 1958
poweriae	0.75–0.85	1	0.17–0.19	segmented	no thin inner shell membrane	Yes	Ahlstrom and Counts, 1958
nimbaria	0.64–0.72	none		irregularly segmented	thin inner shell membrane	No	Ahlstrom and Counts, 1958
attenuata	0.84–0.92	1	0.18–0.195	segmented	no thin inner shell membrane	No	Sanzo, 1931d
Gonostoma denudatum	0.80–0.81	1	0.20–0.21	—	—	No	Sanzo, 1931d

Ahlstrom (1974:672) favored recognition of one family for those stomiiforms with elongate gill rakers in adults. According to the rules of priority this would be the Sternoptychidae. Weitzman (1974:338) recognized three families, Gonostomatidae, Photichthyidae, and Sternoptychidae, for the same stomiiforms, the last family including the "maurolicin" genera formerly assigned to the Gonostomatidae and the deep-bodied sternoptychids traditionally assigned to the family. In a phylogenetic or cladistic analysis this elongate gill raker bearing "group," if recognized as a single family, is paraphyletic if one considers certain of its subgroups as equivalent or higher taxonomic categories. For example, recognition of Ahlstrom's Sternoptychidae, which would include the Stomiidae, a monophyletic group with its members having a median barbel attached to the ventral surface of the head in association with the hyoid bone and lacking elongate gill rakers in adults, is incompatible with a phylogenetic classification based on nested monophyletic groups, since the Stomiidae is the sister group of another group within Ahlstrom's Sternoptychidae. Furthermore, the character used here to "define" the paraphyletic Sternoptychidae, the presence of elongate gill rakers in adults, is excellent for use in a key for identification purposes, but cannot be used as a synapomorphy relating these fishes because it is primitive for stomiiforms. Ahlstrom's Sternoptychidae is undefinable in a phylogenetic analysis based on the information at hand. A resolution of the use of familial and subordinal names in stomiiform fishes must await completion of ongoing phylogenetic studies of these fishes. Because these studies are incomplete, it is difficult to make recommendations for names of certain stomiiform subgroups. Among the stomiiforms with elongate gill rakers in adults, the "family" problem is more complex than that recognized by Ahlstrom (1974) or Weitzman (1974). We here recognize two family names but these apply to only some of the 24 genera listed below. We recognize the Sternoptychidae of Weitzman (1974) and the Gonostomatidae in a new and restricted sense. See discussion below.

The stomiiforms discussed here include the following 24 genera, listed alphabetically, which have been variously recognized as belonging to the families Gonostomatidae, Sternoptychidae, Maurolicidae, and Photichthyidae: *Araiophos* Grey (two species), *Argyripnus* Gilbert and Cramer (four, possibly a few more), *Argyropelecus* Cocco (about seven), *Bonapartia* Goode and Bean (one), *Cyclothone* Goode and Bean (twelve), *Danaphos* Bruun (one, possibly two), *Diplophos* Günther (two), *Gonostoma* Rafinesque (six), *Ichthyococcus* Bonaparte (three), *Manducus* Goode and Bean (two),[1] *Margrethia* Jespersen and Tåning (one, possibly two), *Maurolicus* Cocco (one, possibly two), *Photichthys* Hutton (one), *Pollichthys* Grey (one), *Polyipnus* Günther (about sixteen), *Polymetme* McCulloch (one, possibly four), *Sonoda* Grey (two), *Sternoptyx* Hermann (two or three), *Thorophos* Bruun (two, including *Neophos* Myers), *Triplophos* Brauer (one), *Valenciennellus* Jordan and Evermann (one, possibly two), *Vinciguerria* Jordan and Evermann (five), *Woodsia* Grey (one), and *Yarella* Goode and Bean (one).

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[1] Grey (1964:88) recognized *Manducus* Goode and Bean, 1896 as a junior synonym of *Diplophos* Günther, 1873 because, as she stated ". . . the differences appear to be of a specific rather than a generic nature . . ." This was in the context of the kinds of differences Grey noted separating other species of "gonostomatids." She did recognize both as subgenera of *Diplophos*. We recognize both as genera. The species were most recently reviewed by Mukhacheva (1978) who recognized four species, *D. maderensis* (Johnson), *D. rebainsi* Krefft and Parin, *D. greyae* R. K. Johnson, and *D. taenia* Günther. We have examined all four species and find that *D. taenia* and *D. rebainsi* have the cartilages of the two medial proximal pectoral radials, radials III and IV in the terminology of Fink and Weitzman (1982:66), fused while retaining two bony elements separate as reported for *D. taenia* by Fink and Weitzman (1982:65–67). Furthermore, one of the distal radials is out of line, not in a single series in these two species. These characters are specialized for these species. In *Manducus maderensis* and *M. greyae* there are four completely distinct proximal radials and the distal radials are all in a simple straight series. Because the pectoral radial morphology in *Diplophos taenia* and *D. rebainsi* may be an intermediate stage of a transition series between radials such as are found in *Manducus maderensis* and *M. greyae* and those in the "photichthyid" genera, we recognize *Manducus* as a genus and apparent sister group of the "photichthyid" genera as well as the Stomiidae, nearly all of which have the radials III and IV completely fused to one bone. A few stomiids have an apparent neomorph condition in which the third proximal radial is divided into two radials, giving a total of four proximal radials. See also text discussion.

TABLE 48. SUMMARY OF MERISTIC CHARACTERS FOR ADULTS OF CERTAIN STOMIIFORM FISHES.

Genera	No. species	Fin rays				Branchiostegal rays	No. of vertebrae	No. of gill rakers
		Dorsal	Anal	Pectoral	Pelvic			
Araiophos	2	13–20	20–29	16–18	5	9–11	43–45	2–3 + 12–19 = 14–22
Argyripnus	4+	11–12	11–15 + 8–12 = 22–29	15–19	6–7	8–10	41–46	4–7 + 12–19 = 16–26
Argyropelecus	7	(8) 9 (10)	6–8 + 5–6 = 11–13	10–11	?	?	34–40	15–24
Bonapartia	1	17–20	29–31	14–16	7–8	13–16	37	5–6 + 11–12 = 16–18
Cyclothone	12+	12–15	16–21	9–13	6–7	10–14	29–33	4–10 + 9–18 = 14–27
Danaphos	1	6	24–25	13–14	6	9–10	38	2 + 11–13 = 13–15
Diplophos	2	10–13	47–69	8–9	7	10–14	44–94	3 + 7–9 = 10–12
Gonostoma	6	10–18	21–31	9–13	6–8	10–13	37–40	5–11 + 10–17 = 15–27
Ichthyococcus	3	10–15	13–17	7–8	6–7	11–12	38–47	7–11 + 15–26 = 22–37
Manducus	2	11–13	36–59	9–11	8	11–14	63–76	3–5 + 8–10 = 12–14
Margrethia	1	15–16	21–26	13–15	8	13	34	5 + 10–11 = 15–16
Maurolicus	1	9–12	8–10 + 11–15 = 19–27	17–20	6–7	9–10	33–35	4–8 + 17–22 = 22–30
Photichthys	1	12–13	23–26	9	6–7	20–21	51	4–5 + 11 = 15–16
Pollichthys	1	10–12	22–30	8	6–7	11–12	40	4–5 + 11–12 = 15–17
Polyipnus	17	10–17	13–19	12–16	?	?	31–36	10–28
Polymetme	3	11–13	24–33	9–11	7 (8?)	12–14	44–45	5–8 + 9–12 = 15–19
Sonoda	2	8–9	8–10 + 14–16 = 22–25	13–15	6	8–10	40?	3–5 + 15–18 = 18–21
Sternoptyx	3	8–11	14–16	10–11	?	?	28–31	7–9
Triplophos	1	10–12	53–63	9–11	6–7	11–14	ca 60	9 + 14–16 = 23–25
Thorophos	2	8	38	13	7	7–8	40–45	5 + 13–14 = 18–19
Valenciennellus	2 or 3	7–12	22–25	12–13	6–9	9–10	32–33?	2–3 + 12 = 14–15
Vinciguerria	4	13–16	12–17	9–10	7	10–12	38–42	3 + 11–23–11 = 15–33
Woodsia	1	11–12	14	9–10	7–8	17	42–45	3–5 + 13 = 16–18
Yarella	2	14–16 (17)	(28) 29–31	8–10	6–7	13–16	45–54	6–7 + 12–16 = 18–22

TABLE 49. POSITION OF THE DORSAL AND ANAL FIN AND CONDITION OF THE ADIPOSE FIN IN CERTAIN STOMIIFORM FISHES.

Genus	Dorsal fin position		Adipose fin
	Adult	Larvae	
Araiophos	Anal origin in advance of dorsal fin. Dorsal origin opposite 5th or 6th anal ray	Anal opposite dorsal at 8 mm, adult position at 11 m	Present or absent
Argyripnus	Anal origin opposite dorsal origin	Anal origin opposite dorsal origin	Present
Argyropelecus	Anal origin opposite last dorsal fin ray	Anal origin behind dorsal fin	Present or absent
Bonapartia	Anal origin well in advance of dorsal by 9 rays	Same as adult	Absent
Cyclothone	Anal origin opposite dorsal fin or slightly behind	Same as adult	Absent
Danaphos	Anal origin behind dorsal fin	Same as adult	Absent
Diplophos	Anal origin beneath 5th ray or behind dorsal fin	Anal origin beneath end of or behind dorsal fin	Absent
Gonostoma	Anal origin opposite or 3–4 rays in advance of dorsal origin	Same as adult	Present or absent
Ichthyococcus	Anal origin behind dorsal fin by a space = ½ dorsal base	Anal origin behind dorsal fin	Present
Manducus	Anal origin beneath 3rd from last or last dorsal fin ray	Unknown	Absent
Margrethia	Anal origin beneath 5th dorsal fin ray	Same as adult	Present
Maurolicus	Anal origin beneath last dorsal fin ray	Anal origin beneath middle of dorsal fin, advances to adult condition as juveniles	Present
Photichthys	Anal origin behind dorsal fin	Unknown	Present
Pollichthys	Anal origin beneath 3rd dorsal fin ray	Anal origin advances forward beneath dorsal fin	Present
Polyipnus	Anal origin usually beneath middle of dorsal fin	Same as adult	Present or absent
Polymetme	Anal origin beneath end of dorsal fin	Unknown	Present
Sonoda	Anal origin in advance of dorsal. Dorsal origin above 5th anal ray	Unknown	Absent
Sternoptyx	Anal origin opposite dorsal origin	Anal origin behind dorsal fin	Present
Triplophos	Anal origin beneath end of dorsal fin	Unknown	Absent
Thorophos	Anal origin in advance of dorsal origin by 3 or 4 rays	Unknown	Present or absent
Valenciennellus	Anal origin 1 or 2 rays in advance of dorsal origin	Same as adult	Present
Vinciguerria	Anal origin beneath middle of dorsal fin	Same as adult	Present
Woodsia	Anal origin behind middle of dorsal fin by distance about = dorsal base	Same as adult	Present
Yarella	Anal origin beneath middle of dorsal fin	Same as adult	Absent

Table 50. Definition of Alphabetical Symbols used for Designating Photophores in Deep Bodied Sternoptychids and Other Stomiiform Fishes.

Other stomiiforms		Deep bodied sternoptychids	
Code	Definition	Code	Definition
SO	Symphyseal photophores (organs) located at tip of lower jaw.	SO	Subopercle photophore which is equivalent to posteriomost photophore in opercular series of gonostomatids.
Orb	Photophores associated with the eye located anterior and posterior of orbit.	PO	Photophore located anterior to orbit.
Op	Photophores on opercle series generally three, coded as follows 1/(1 + 1).	PTO	Photophore located posterior to orbit and may be equivalent to upper photophore of opercular series of gonostomatids.
Br(BRP)	Photophores located on the branchiostegal membranes.	PRO	Preopercular photophore, used for an PO photophore dorsal to ventral limb or preopercle.
Is(I)	Photophores located on the isthmus.	Br	Same as gonostomatid definition.
IP	Photophores of the ventral series found from the isthmus to the base of the pectoral fin.	Is	Same as gonostomatid definition.
PV	Photophores of the ventral series found from the pectoral fin base to the pelvic (ventral) fin base.	AB	Photophores of ventral series located abdominally between pectoral fin base and pelvic fin base and equivalent to PV in gonostomatids, plus a few posterior photophores of the IP series.
VAV	Photophores of the ventral series found from the pelvic (ventral) fin base to the anal fin base.	PAN	Photophores found anterior to anal fin and may be equivalent to VAV or VA in gonostomatids.
AC	Photophores of the ventral series found from the anal fin base to caudal fin base of the ventral series.	AN	Photophores found above anal fin.
		SC	Photophores found on lower (sub) caudal peduncle. Together with AN group may be equivalent to AC in gonostomatids.
IC	Summary of photophores of the ventral series from the isthmus to caudal fin base (IP+PV+VAV+AC).	SAB	Photophores located above (supra) to the abdominal series and may be equivalent to VA in gonostomatids.
IV	Summary of photophores of the ventral series from isthmus to pelvic (ventral) fin base (IP+PV).	SP	Photophores located above (supra) the pectoral fin and may be equivalent to OV in gonostomatids.
OV	Photophores of the lateral series from the opercle to pelvic (ventral) fin base.	L	Photophore located laterally above PAN (found only in *Polyipnus*).
VA(VALA)	Photophores of the lateral series from the pelvic (ventral) fin base to the anal fin base.	SAN	Photophores located above (supra) to anal photophores and equivalent to part of AC series.
OAA	Summary of photophores of OV plus VA series.		
OA(OAB)	Summary of lateral photophores from the opercle to anal fin base (OV+VA).		
OAC(OC)	Entire lateral series on body sides just dorsal to ventral series and extending from opercular border, or just medial to it, over anal fin to caudal fin base.		
ODM	Photophores (organs) found dorsal to the lateral midline (found only in *Gonostoma gracile*).		

Some genera are extremely rare (i.e., *Thorophos* and *Sonoda*) while others represent the most abundant vertebrate animals on earth (*Cyclothone* and *Vinciguerria*).

Developmental information has been published for 16 of these genera (12 prior to Ahlstrom, 1974; 3 by Ahlstrom, 1974; and one by Ozawa, 1976).

Development

Eggs.—Eggs were described for *Argyropelecus hemigymnus* by Sanzo (1928); for *Ichthyococcus ovatus* by Sanzo (1930b); for *Maurolicus muelleri* by Sanzo (1931d), Mito (1961a), and Okiyama (1971); for *Vinciguerria lucetia, V. poweriae,* and *V. nimbaria* by Ahlstrom and Counts (1958); for *V. attenuata* by Sanzo (1931d); and for *Gonostoma denudatum* by Sanzo (1931d). Other accounts provide minimal details of ovarian eggs of other species. The details of egg characters are summarized in Table 47.

Larvae.—Much has been accomplished for the identification of the larvae of these stomiiform genera and now descriptions are available for all except *Manducus, Triplophos, Polymetme, Photichthys, Thorophos,* and *Sonoda.* The larvae tentatively identified as *Polymetme* by Ahlstrom (1974), on further examination by one of us (Richards), were determined to be *Pollichthys.* One stomiiform larval form has been described but not assigned to a genus [designated "Maurolicine Alpha" by Ahlstrom (1974: 670)]. It presumably is the larva of some sternoptychid (as defined by Weitzman, 1974). Descriptive details and illustrations of several species were given by Ahlstrom (1974). Here we provide new or additional data including characters useful in identifying these larvae and illustrations of all the species described to date, including some illustrated for the first time.

The identification of stomiiform larvae with elongate gill rakers as adults requires a knowledge of developmental data from larvae, juveniles, and data from adults of the following characters: counts of fin rays, teeth, and other meristic characters as photophores; patterns of photophore development; and distributions (patterns) of dark chromatophores (dark pigment cells). With those sets of data, nearly all species should be identifiable at least to genus, and in cases of complete data, to species. A

TABLE 51. PHOTOPHORE DISTRIBUTION IN CERTAIN STOMIIFORM GENERA. Refer to text and Table 50 for definition of codes.

	No. of rows	SO	ORB	OP	BR	IS	IV	VAV	AC	Photophores in group of glands
Araiophos	1	No	1	1	5–7	Yes	(2) + (3) + 3–4 + (2) = 10–11	3–5	6–8	Yes
Argyripnus	2	No	1	3	6	Yes	(6) + (10)	(18–28)	(4–5) + (12–18) = 35–51	Yes
Argyropelecus	2	No	2	2	6	Yes	18	4	10	Yes
Bonapartia	1	Yes	1	3	11–13	No	14–16	5–6	18–20	No
Cyclothone	2	No	1	2	8–11	No	12–14	4–5	12–16	No
Danaphos	2	No	1	2–3	6	Yes	18	5	22–26	Yes
Diplophus	3+	Yes	1	3	7–12 + 0–3	Yes	33–49	13–17	33–49	No
Gonostoma	2	Yes	1	2–3	9	No	11–16	3–10	15–23	No
Ichthyococcus	2	No	2	3	11–12	Yes	25–28	9–14	12–14	No
Manducus	2+	Yes	1	3	8–13	Yes	30–33	12–14	28–39	No
Margrethia	1	No	1	3	9–12	No	13–15	4	17	No
Maurolicus	2	Yes	1	3	(6)	Yes	(6) + (12–13) = 18–19	(6)	1 + (14–18) + (7–9) = 22–27	Yes
Photichthys	2	Yes	2	3	17–18	Yes	10 + 14–15 = 24–25	15–17	16–18	Yes
Pollichthys	2	Yes	2	3	8	Yes	21–23	7–9	18–21	No
Polyipnus	2	No	2	2	6	Yes	16	5	10–18	Yes
Polymetme	2	Yes	1	3	9–10	Yes	19–21	7–8	21–25	No
Sonoda	2	No	1	3	6–7	Yes	6 + 10 = 16	7–8	(16–21) + (19–24) or (5–6) + (5–6) + (5–6) = 36–43	Yes
Sternoptyx	2	No	2	2	3	Yes	15	3	7	Yes
Triplophos	2 + 3 or 4	Yes	1	3	8–13	Yes	24–30	5–7	35–41	No
Thorophos	2	Yes & no	1	3	6	Yes	17	5	13–15	Yes
Valenciennellus	2	No	1	3	6	Yes	(3) + (4) + (16–17) = 23–24	(4)–(5)	3–6 or 9–17	Yes
Vinciguerria	2	Yes or no	2	3	7–9	Yes	21–24	7–11	12–15	No
Woodsia	2	Yes	2	3	14	Yes	25	11–12	12	No
Yarella	2+ sev	Yes	1	3	11–13	Yes	23–25	9–12	20–28	No

summary of several meristic characters for genera is given in Table 48. The position of the dorsal and anal fins is also a helpful aid, but caution must be used since their positions relative to other structures may change with growth. Also, the presence or absence of the adipose fin is helpful, but again, caution is in order because this fin is fragile and often damaged or lost due to contact with a net. These fin features are given in Table 49. Of special importance in identifying larvae and adults is the distribution and patterns of the photophores. This includes the number in each series, the patterns of their distribution in relation to each other, and especially the sequence of development which Ahlstrom (1974) stressed. Some confusion appears in the literature because more than one alphanumeric code has been developed to indicate, in some cases, the same sets of photophores in different stomiiform groups. A further complication is that the deep-bodied sternoptychids have a different code because of their altered body shape as adults and homologies were considered uncertain. Weitzman (1974:461), because he united the "maurolicin" and deep-bodied stomiiforms as one family considered the different terminologies "artificial" and as obscuring homologies. He therefore discussed and presented a synonymy of stomiiform photophores. We have defined the alphabetical codes in Table 50 and included what we believe are equivalent photophores in stomiiforms. In this code, parenthetical numbers indicate photophores found in common glands whereas non-parenthetical numbers indicate that the photophores are single. The distribution of photophores for each genus is given in Table 51. Table 52 provides sequences of photophore formation for *Bonapartia, Margrethia,* and *Gonostoma.* Table 53 provides similar information for *Araiophos, Maurolicus, Danaphos, Valenciennellus,* and *Argyripnus*; while Table 54 provides similar data for *Polyipnus, Argyropelecus,* and *Sternoptyx.* Diagnostic pigmentation and morphometric characters are summarized in Table 55. Illustrations (Figs. 98 to 104) are provided for the genera for which larvae are known and for many of the known species. In addition, the following authors provide specific information which will aid in larval identifications: Jespersen and Tåning (1919, 1926), Sanzo (1931d), Ahlstrom and Counts (1958), Ahlstrom and Moser (1969), Ozawa (1976), Grey (1964), Badcock and Merrett (1972), Kawaguchi and Marumo (1967), Okiyama (1971), Badcock (1982), Rudometkina (1981), Gorbunova (1981), Mukhacheva (1964), and Ahlstrom (1974).

RELATIONSHIPS

There has been a dichotomy of opinions about the interrelationships of the genera and the use of family names based on the use of larval versus adult morphological characters. Ahlstrom (1974:670–672) presented his views on this group based on larval characters, principally the mode of photophore formation. The suggested relationships resulting from his analysis contrasted in part with those of Weitzman (1974:472), whose views were based on study of adult osteology and soft anatomy Both Ahlstrom and Weitzman in addition to their own data,

TABLE 52. Sequence of Photophore Formation in *Bonapartia, Margrethia,* and *Gonostoma.*

		ORB	OP	SO	BR	PV	VAV	AC	OA + ODM	Source
Bonapartia pedaliota	adult	1	3	1	11–13	14–15	5–(6)	16–18 + 2–3	0	Grey, 1964
	9.5	0	1	0	2	3	0	0	0	Grey, 1964
	11.5	0	1	0	3	5	2	0	0	Original
	12.0	0	1	0	4	5	2	0	0	Grey, 1964
	14.0	1	1	0	5	10	4	3 + 1	0	Grey, 1964
	15.0	1	1	0	5	9	3	1 + 1	0	Original
	16.0	1	1	0	6	11	5	5 + 2	0	Jespersen and Tåning, 1919
	23.0	1	3	0	11	14	5	14 + 2	0	Grey, 1964
Margrethia obtusirostra	adult	1	3	0	9–12	13–15	4	13–14 + 3–4	0	Grey, 1964
	5.8	0	1	0	0	2	0	0	0	Ahlstrom, 1974
	6.4	0	1	0	0	6	2	1 + 2	0	Ahlstrom, 1974
	8.0	0	1	0	2	10	4	1 + 2	0	Ahlstrom, 1974
	11.3	—	2	0	6	14	4	5 + 3	0	Ahlstrom, 1974
	15.0	1	3	0	9	14	4	11 + 4	0	Ahlstrom, 1974
Gonostoma elongatum	adult	1	3	1	9	15	(4)–5	21–23	13–15	Grey, 1964
	6.0	0	1	0	0	0	0	0	0	Ahlstrom, 1974
	7.5	0	1	0	0	5	0	0	0	Ahlstrom, 1974
	7.9	0	1	0	0	4	0	0	0	Original
	10.2	0	1	0	2/1	10	2	0	0	Ahlstrom, 1974
	13.0	0	1	0	2	11	3	0	0	Ahlstrom, 1974
	14.0	1	1	0	2	11	2/3	1+	0	Grey, 1964
	16.7	1	1	0	3	11	4	1+	0	Jespersen and Tåning, 1919
	22.5	1	3	1	9	15	5	22	13	Grey, 1964
Gonostoma denudatum	adult	1	3	1	9	15–16	5	17–20	13–15	Grey, 1964
	18.25	0	1	0	0	1	0	0	0	Sanzo, 1912b
	19.0	0	1	0	0	2	0	+2	0	Sanzo, 1912b
	20.75	0	1	0	1	3	1	+3	0	Sanzo, 1912b
	24.75	0	1	0	3	6	3	3 + 3	0	Sanzo, 1912b
	29.65	0	2	0	5	14	5	11 + 3	0	Sanzo, 1912b
	34.0	1	3	0	9	16	5	15 + 5	13	Sanzo, 1912b
	39.0	1	3	1	9	16	5	15 + 5	13	Sanzo, 1912b
Gonostoma gracile	adult	1	2	1	9	13–15	4–5	17–19	11–12 + 6–7	Kawaguchi and Marumo, 1967
	15.5–5–17.0	0	1	0	0	0	0	0	0	Kawaguchi and Marumo, 1967
	20.0	1	2	1	2	13	5	17	0	Kawaguchi and Marumo, 1967
	22.0	1	2	1	9	14	4	18	12 + 4	Kawaguchi and Marumo, 1967
Gonostoma ebelingi	adult	1	2	1	9	15	10	19	21	Grey, 1964
	13.8	0	1	0	0	7	0	0	0	Ahlstrom, 1974
	15.0	0	1	0	0	9	0	0	0	Ahlstrom, 1974
Gonostoma bathyphilum	adult	1	2	0	9	11–12	4–5	20–21	14	Grey, 1964
	11.0	0	1	0	0	5	0	0	0	Ahlstrom, 1974
	14.8	1	1	0	4	10	2	0	0	Ahlstrom, 1974
Gonostoma atlanticum	adult	1	2	1	9	15–16	5	19	13	Grey, 1964
	12.0	0	1	0	0	0	0	0	0	Ahlstrom, 1974
	13.0	0	1	0	0	1	0	0	0	Ahlstrom, 1974
	14.5	0	1	0	0	2	0	0	0	Ahlstrom, 1974
	17.8	1	1	0	4	13	3	1	0	Original
	18.8	1	2	0	9	16	5	19	0	Ahlstrom, 1974
	23.8	1	3	0	9	16	5	19	13	Original

used the results of photophore anatomy research by Bassot (1966, 1971) to support their conclusions. These results seemingly completely supported Weitzman's referral of genera to family groups and agreed with Ahlstrom except for placement of three genera—*Cyclothone, Diplophos* (including *Manducus*), and *Triplophos.*

One of us (Weitzman), continues to study relationships of the stomiiforms with elongate gill rakers in adults and we offer the following analysis as a current comment on the status of our knowledge of these fishes. The two concepts of relationships by Ahlstrom and Weitzman may be compared as follows: Ahlstrom (1974:670–672) stressed relationships of taxa based on photophore patterns and development. Ahlstrom (1974:672) considered the stomiiforms with elongate gill rakers in adults as a group comprised of three groups of genera, with any subdivision being into two subfamilies based on photophores occurring individually or in clustered groups. These groups of genera include: (1) Those with individual separate photophores, most of the photophores developing simultaneously and initiated as a "white" photophore stage. This group includes *Manducus, Diplophos, Cyclothone, Yarella, Pollichthys, Vinciguerria, Woodsia, Ichthyococcus,* and presumably *Triplophos* and *Polymetme,*

TABLE 53. SEQUENCE OF PHOTOPHORE FORMATION IN *ARAIOPHOS, MAUROLICUS, DANAPHOS, VALENCIENNELLUS,* AND *ARGYRIPNUS.*

		ORB	OP	SO	BR	IP	PV	VAV	AC	OA	Source
Araiophos eastropas	adult	1	1	0	(6)	(2)	(3) + 3–4 + (2)	(3)	(2) + 2 + (2)	No	Ahlstrom and Moser, 1969
	11.2	0	0	0	(3)	0	(2)	0	0	—	Ahlstrom and Moser, 1969
Maurolicus muelleri	adult	1	3	1	(6)	(6)	(12)	(6)	3/(4) + (8)	(2) + 7	Ahlstrom, 1974
	5.5	0	0	0	(1/2)	0	0	0	0	0	Ahlstrom, 1974
	6.2	0	0	0	(2)	0	(2)	0	0	0	Ahlstrom, 1974
	6.5	0	0	0	(2)	0	(4)	0	0	0	Ahlstrom, 1974
	6.7	0	1	0	(3)	0	(5)	0	0	0	Ahlstrom, 1974
	6.9	1	1	0	(4)	0	(8)	0	0	0	Ahlstrom, 1974
	7.5	1	1	0	(4)	1	(9)	0	0 + (2) + 0	0	Ahlstrom, 1974
	8.6	1	2	0	(5)	(3)	(12)	(2)	0 + (3) + (3)	0	Ahlstrom, 1974
	9.0	1	2	0	(5)	(3)	(11)	(2)	0 + (3) + (3)	1	Ahlstrom, 1974
	9.7	1	3	0	(5)	(5)	(11)	(3)	0 + (4) + (6)	(2) + 1	Ahlstrom, 1974
	10.8	1	3	0	(6)	(5)	(12)	(4)	0 + (5) + (6)	(2) + 2	Ahlstrom, 1974
	13.5	1	3	0	(6)	(6)	(12)	(6)	0 + (9) + (7)	(2) + 6	Ahlstrom, 1974
Danaphos oculatus	adult	1	3	0	(6)	(3) + (4)	(11)	(5)	(3) + 16 + (4) + 1	6	Ahlstrom, 1974 Ahlstrom, 1974
	16.5	0	0	0	(2)	0	0	0	0	0	Ahlstrom, 1974
	16.5	0	0	0	(3)	0	(3)	0	0	0	Ahlstrom, 1974
	19.2	0	0	0	(4)	0	(10)	0	0	0	Ahlstrom, 1974
	21.0	1	1	0	(5)	(2) + (4)	(10/11)	0	(2) + 0 + 0 + 0	0	Ahlstrom, 1974
	21.3	1	1	0	(4/5)	(3) + (4)	(10)	0	(3) + 0 + (2) + 0	0	Ahlstrom, 1974
	21.8	1	2	0	(5)	(3) + (4)	(11)	(2)	(3) + 8 + (4) + 0	2	Ahlstrom, 1974
	24.2	1	2	0	(6)	(3) + (4)	(11)	(2)	(3) + 9 + (4) + 0	2	Ahlstrom, 1974
Valencinnellus tripunculatus	adult	1	3	0	(6)	(3) + (4)	(16–17)	(4–5)	(3) + (3) + (3) + (2) + (4)	(2) + 3	Ahlstrom, 1974
	7.8	0	0	0	0	0	0	0	0	0	Original
	8.6	0	0	0	(3)	0	(3)	0	0	0	Ahlstrom, 1974
	9.5	0	0	0	(4)	0	(6)	0	0	0	Ahlstrom, 1974
	11.0	0	0	0	(4)	0	(10)	0	0	0	Original
	12.0	0	0	0	(4)	0	(13)	(2)	0	0	Ahlstrom, 1974
	12.4	1	0	0	(5)	0	(15)	(2)	0	0	Original
	13.0	1	0	0	(5)	(2)	(15)	(2)	0	0	Original
	13.2	0	0	0	(4)	0	(14)	(3)	0	0	Ahlstrom, 1974
	14.0	1	0	0	(5)	(4)	(15)	(5)	0	0	Original
	17.0	1	2	0	(4–5)	(3) + (4)	(15)	(5)	(3) + (3) + 0 + (3) + (4)	(2)	Grey, 1964
Argyripnus atlanticus	adult	1	3	0	(6)	(6)	(10)	(26)	(5) + (17)	(3) + 4	Badcock and Merrett, 1972
	18.7	1	2	0	(6)	(3)	(10)	(3)	(4) + (4)	0	Badcock and Merrett, 1972
	16.8	1	2	0	(6)	(3)	(10)	(2)	(4) + (3)	0	Badcock and Merrett, 1972

although their development is not known. (2) Those with individual, separate photophores that have a gradual, protracted metamorphosis. This group includes *Bonapartia, Margrethia,* and *Gonostoma.* (3) Those with some individual photophores but some or most of the photophores with common bases [actually a common lumen, during development at least] and having a gradual, protracted metamorphosis. This group includes *Araiophos, Maurolicus, Danaphos, Valenciennellus, Argyripnus, Polyipnus, Argyropelecus, Sternoptyx,* and presumably *Thorophos* and *Sonoda* although their development is unknown. Groups (1) and (2) comprised the subfamily Gonostomatinae and Group (3) comprised the Sternoptychinae in Ahlstrom's concept. Group (3) is equivalent to Weitzman's Sternoptychidae. The genus *Gonostoma* was considered "pivotal" by Ahlstrom; that is, its relationships could be with either the gonostomatines or the sternoptychines of his concept. In Ahlstrom's conclusions, the photophore pattern of Group (1) is most like that of the stomiid groups discussed by Fink in this volume.

Weitzman's classification (1974) concentrated in most detail on a hypothesis of phylogenetic relationships within the family Sternoptychidae as he defined it. Weitzman (1974) pointed out that more detailed studies should be conducted on other stomiiform genera in the future, but he did discuss their possible relationships. Based on the number of proximal pectoral-fin radials, he established two infraorders for stomiiform fishes. Members of the Infraorder Gonostomata were considered to have four proximal pectoral-fin radials (except *Cyclothone* with one). This infraorder was divided into two families based principally on Bassot's photophore findings; Family Gonostomatidae with Beta type photophores comprised of *Diplophos* including *Manducus*), *Triplophos, Bonapartia, Margrethia, Gonostoma,* and *Cyclothone* and the Family Sternoptychidae with Alpha type photophores comprised of *Thorophos, Araiophos, Maurolicus, Danaphos, Valenciennellus, Argyripnus, Sonoda, Polyipnus, Argyropelecus,* and *Sternoptyx.* The problem with Weitzman's Gonostomata is that it was based on a primitive character for the stomiiforms, four pectoral-fin radials, and this character cannot be used as a synapomorphy to define a subgroup of stomiiforms. The non-sternoptychid and non-gonostomatid genera, along with the stomiiform families possessing barbels originating from the hyoid bone and lacking elongate gill rakers in the adults (the Stomiidae of Fink, this volume),

TABLE 54. SEQUENCE OF PHOTOPHORE FORMATION IN *POLYIPNUS, ARGYROPELECUS* AND *STERNOPTYX*.

	Size	PO	PTO	BR	IS	OP PRO + SO	SP	AB	SAB	PAN	AN	SAN	LSC	Source
Polyipnus polli	adult	1	1	6	6	1 + 1	3	10	3	5	8	3	14	Baird, 1971
	4.3	0	0	2	0	0 + 1	0	1	0	0	0	0	0	Original
	4.8	1	0	4	2	1 + 1	0	3	0	0	0	0	0	Original
	5.5	1	1	6	4	1 + 1	2	8	0	0	0	0	0	Original
	6.0	1	1	6	6	1 + 1	2	10	0	1	0	0	0	Original
	7.5	1	1	6	6	1 + 1	2	10	0	3	0	0	0	Original
	9.0	1	1	6	6	1 + 1	2	10	0	3	2	0	2	Original
	9.6	1	1	6	6	1 + 1	2	10	1	3	2	0	2	Original
	13.5	1	1	6	6	1 + 1	3	10	3	5	4	0	14	Original
	15.3	1	1	6	6	1 + 1	3	10	3	5	4	1	14	Original
	17.0	1	1	6	6	1 + 1	3	10	3	5	4	2	14	Original
	18.4	1	1	6	6	1 + 1	3	10	3	5	6	3	14	Original
	23.5	1	1	6	6	1 + 1	3	10	3	5	7	3	14	Original
Argyropelecus hemigymnus	adult	1	1	6	6	1 + 1	2	12	6	4	6	0	4	Baird, 1971
	10.92	0	0	4	6	0 + 1	0	7	0	0	1	0	2	Sanzo, 1931d
	9.92	0	0	6	6	0 + 1	0	9	0	0	2	0	3	Sanzo, 1931d
	7.84	1	0	6	6	1 + 1	2	12	0	0	3	0	4	Sanzo, 1931d
	11.20	1	1	6	6	1 + 1	2	12	2	3	4	0	4	Sanzo, 1931d
Arygropelecus sp.	adult	1	1	6	6	1 + 1	2	12	6	4	6	0	4	Baird, 1971
	4.5	0	0	0	0	0 + 0	0	0	0	0	0	0	0	Original
	9.5	0	0	6	6	~~0 + 1~~	0	6	0	0	1	0	0	Original
	9.5	0	0	6	6	0 + 1	0	8	0	0	3	0	0	Original
	7.0	1	0	6	6	1 + 1	2	12	0	0	3	0	3	Original
	7.0	1	0	6	6	1 + 1	2	10	0	0	3	0	4	Original
	7.4	1	1	6	6	1 + 1	2	12	4	4	4	0	3	Original
	10.0	1	1	6	6	1 + 1	2	12	5	4	5	0	4	Original
Sternoptyx sp.	adult	1	1	3	5	1 + 1	3	10	0	3	3	1	4	Baird, 1971
	4.8	0	0	0	0	0 + 1	0	0	0	0	0	0	0	Original
	7.5	0	0	0	0	0 + 1	0	0	0	0	0	0	0	Original
	7.8	0	1	2	3	0 + 1	0	4	0	0	0	0	0	Original
	8.1	0	1	2	4	0 + 1	2	7	0	0	0	0	0	Original
	7.6	0	1	2	5	0 + 1	3	10	0	1	3	0	1	Original

TABLE 55. DIAGNOSTIC PIGMENT CHARACTERS AND UNUSUAL MORPHOMETRIC FEATURES OF SOME STOMIIFORM LARVAE.

Genus/species	Diagnostic character
Diplophos taenia	Pigment spots on dorsal and ventral midline. Extremely elongated larvae.
Bonapartia pedaliota	Similar to *Gonostoma* but lacks deep pigment spot behind eyes and has pigment on medial portion of caudal peduncle.
Margrethia obtusirostre	A distinct vertical streak of pigment on caudal peduncle in most specimens.
Gonostoma	All species usually have deep pigment spot behind eyes. Specific differences among the species are as follows: *G. elongatum, G. gracile* and *G. ebelingi* lack pigment on caudal peduncle; *G. bathyphilum* has pigment spots on dorsal edge of caudal peduncle; *G. atlanticum* has pigment over medial portion of caudal peduncle (closely resembles *Cyclothone* in ventral pigmentation and swimbladder position); *G. denudatum* has broad streak of pigment diagonally over caudal fin base from dorsal caudal peduncle to base of lower caudal fin rays.
Cyclothone	A distinct, dark streak or intense melanophore over and parallel to the parhypural on the caudal fin base, pigmentation over gut and along ventral margin of tail and a conspicuous swimbladder.
Yarella blackfordi	Myosepta pigmented over caudal peduncle giving chevron appearance.
Pollichthys mauli	No pigment except for the eyes. Very similar to *Vinciguerria* in other aspects.
Vinciguerria	All species have medial or ventral margin caudal pigment spot. *V. nimbaria* and *V. lucetia* have the caudal pigment spot restricted to the ventral margin of the caudal fin base and pigment above the anal fin. *V. attenuata* and *V. poweriae* has the caudal pigment spot in a medial position and no pigment above the anal fin. *V. attentuata* has pigment over the airbladder which is lacking in *V. poweriae. V. poweriae* has a structure above the anal papilla which may appear as pigment. *V. mabahiss* is similar to *V. nimbaria* and is restricted to the Red Sea (Johnson and Feltes, 1984).
Woodsia nonsuchae	Melanophores profusely distributed on all myomeres below the lateral midline. Broad pigment band along roof of mouth continuous with trunk pigment. Also has a trailing gut and elongated rays on pectoral fin, both of which may be missing.
Ichthyococcus ovatus	Pigment profusely distributed on all myomeres below the lateral midline. Elongate pectoral fin rays and a trailing gut, both of which may be missing.

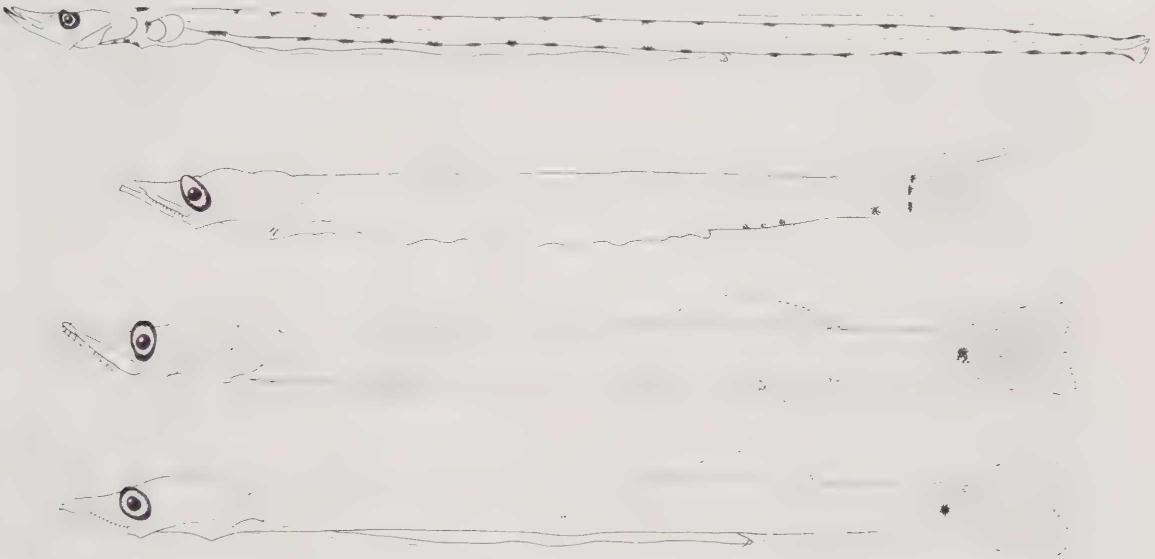


Fig. 98. Lateral views from top to bottom: *Diplophos taenia* 22.0 mm SL, R/V OREGON II Cr. 126, Sta. 36754, 27°30′N, 092°30′W, May 10, 1982, drawn by J. C. Javech; *Vinciguerria lucetia* 9.0 mm SL modified after Ahlstrom and Counts (1958); *Vinciguerria poweriae* 11.5 mm SL, R/V OREGON II Cr. 126, Sta. 36746, 27°59.9′N, 088°00′W, May 8, 1982, drawn by J. C. Javech; and *Vinciguerria attenuata* 9.7 mm SL modified after Jespersen and Tåning (1926).

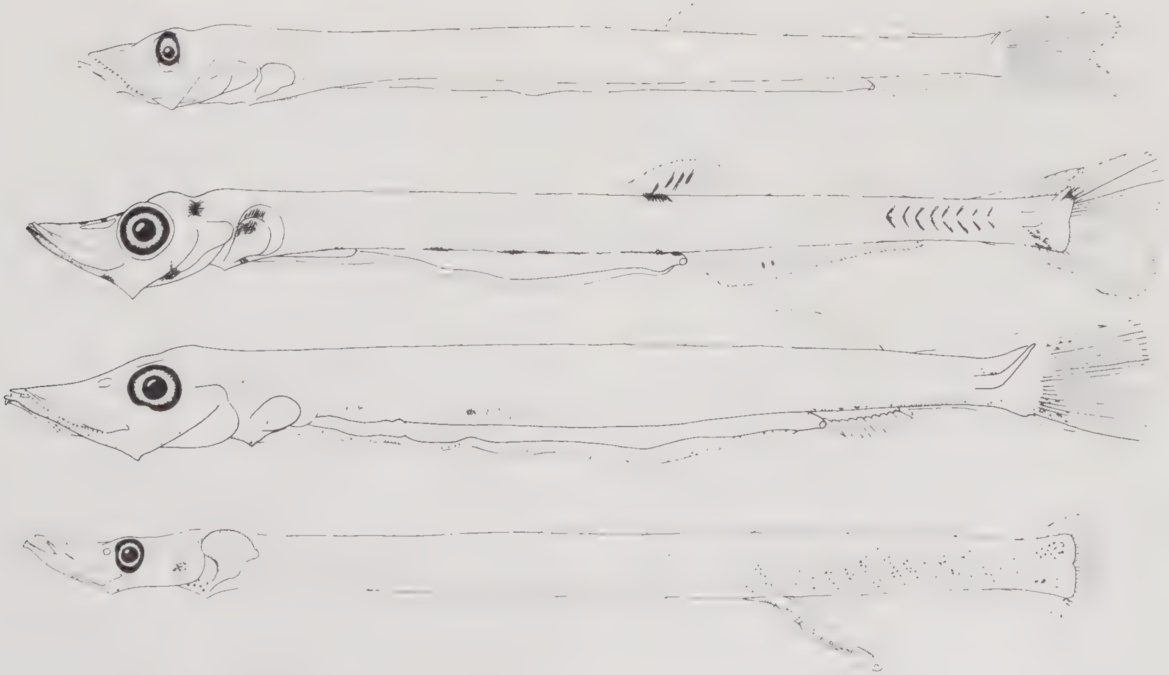


Fig. 99. Lateral views from top to bottom: *Pollichthys mauli* 14.5 mm SL, R/V OREGON II Cr. 126, Sta. 36688, 26°00.5′N, 0.88°00.4′W, April 20, 1982, drawn by J. C. Javech; *Yarella blackfordi* 23.5 mm SL, R/V OREGON II Cr. 126, Sta 36752, 27°30′N, 094°30.3′W, May 9, 1982, drawn by J. C. Javech; *Woodsia nonsuchae* 11.5 mm SL, Eastropac, Sta. 75.225, drawn by J. C. Javech; and *Ichthyococcus ovatus* 18.1 mm SL, R/V OREGON II Cr. 126, Sta. 36746, 27°59.9′N, 0.88°00′W, May 8, 1982, drawn by J. C. Javech.

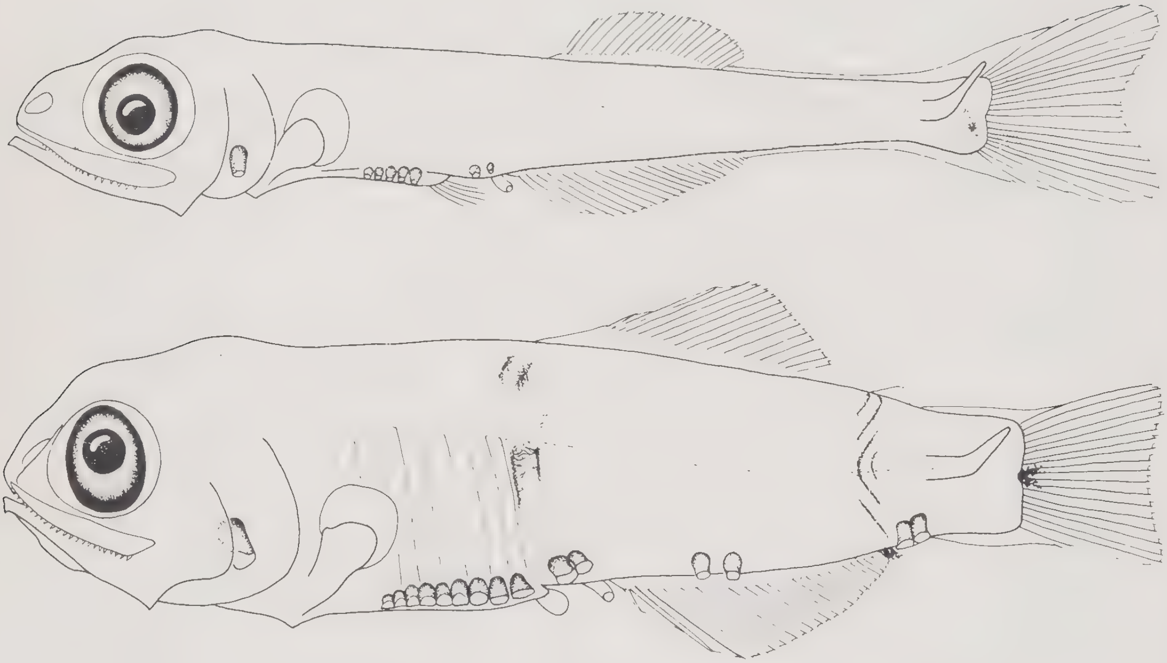


Fig. 100. Lateral views from top to bottom: *Bonapartia pedaliota* 11.5 mm SL, R/V OREGON II Cr. 126, Sta. 36688, 26°00.5′N, 088°00.4′W, April 20, 1982, drawn by J. C. Javech; *Margrethia obtusirostra* 6.7 mm SL, R/V OREGON II Cr. 126, Sta. 36773, 26°00.1′N, 094°00.2′W, May 23, 1982, drawn by J. C. Javech.

were placed in the Infraorder Photichthya. Nearly all have three, or rarely fewer, proximal pectoral-fin radials, a specialized character which can be used as a synapomorphy uniting this group. As noted above, there are a few exceptions which bear four proximal radials but these appear to be either reversals or are neomorphic. Within the Infraorder Photichthya the stomiiform genera with elongate gill rakers in adults were placed in the Family Photichthyidae comprised of the genera *Polymetme, Yarella, Pollichthys, Photichthys, Vinciguerria, Woodsia,* and *Ichthyococcus.* This placement was done on the basis of the presence of Type Gamma photophores in at least most of the genera, a specialization for the group (as well as for at least some of the stomiid genera) and therefore a synapomorphy. The presence of elongate gill rakers in this group is not a synapomorphy because it is primitive for the group.

Essentially, Ahlstrom and Weitzman disagreed on the relationships of three genera. Alhstrom's Group (1) was mostly equivalent to Weitzman's Photichthyidae but included three genera, *Cyclothone, Diplophos* (including *Manducus*), and *Triplophos,* placed in the Gonostomatidae by Weitzman. Otherwise, Weitzman's Gonostomatidae was equivalent to Ahlstrom's Group (2). Based on evidence available to Ahlstrom and Weitzman, on some supplementary evidence provided by Fink and Weitzman (1982), and on some of our own data, we here present a somewhat different arrangement based on a more rigorous phylogenetic analysis than done by Weitzman (1974). It turns out that Weitzman's analysis of the Sternoptychidae and its genera is consistently phylogenetic but that of outgroup stomiiforms is not. Ahlstrom (1974) did not attempt to analyze his groups phylogenetically. The evidence available now seems to resolve the conflict between Ahlstrom (1974) and Weitzman (1974). However, we would note that the analysis below is to be regarded as a guide to future studies rather than any sort of well-corroborated phylogeny. Parts, at least, of the arrangement need much additional study. Furthermore, the relationships of the genera in contention by Ahlstrom and Weitzman are still not fully clear. Some of these genera, *Manducus, Diplophos,* and perhaps *Triplophos,* are relatively primitive within stomiiforms with few characters specialized beyond the stomiiform level. This makes placing them in stomiiform subgroups difficult. *Cyclothone* is more derived but retains certain primitive stomiiform features and its relationship, although in our view is undoubtedly with the gonostomatids, at this time is somewhat uncertain because our data are not fully analyzed.

The conflict between Ahlstrom (1974) and Weitzman (1974) arose in part because they both utilized one or the other of certain characters, Type Beta photophores and "white" photophore development, as though they were shared specialized characters, synapomorphies indicating relationships. Instead, we believe these features are plesiomorphous for stomiiform subgroups and cannot be used to support a hypothesis of relationships among stomiiform genera. Our current analysis is as follows.

Fink and Weitzman (1982:69–75) list and discuss eight synapomorphies for stomiiform fishes. One of these, stomiiform-type photophores, was described in some detail based in part on Bassott (1966, 1971). Bassot (1966:574–576), Weitzman (1974:338), and Fink and Weitzman (1982:70) recognized Type Beta photophores as primitive for stomiiforms. Bassot (1966, 1971) recognized two other types of photophores, Type Alpha

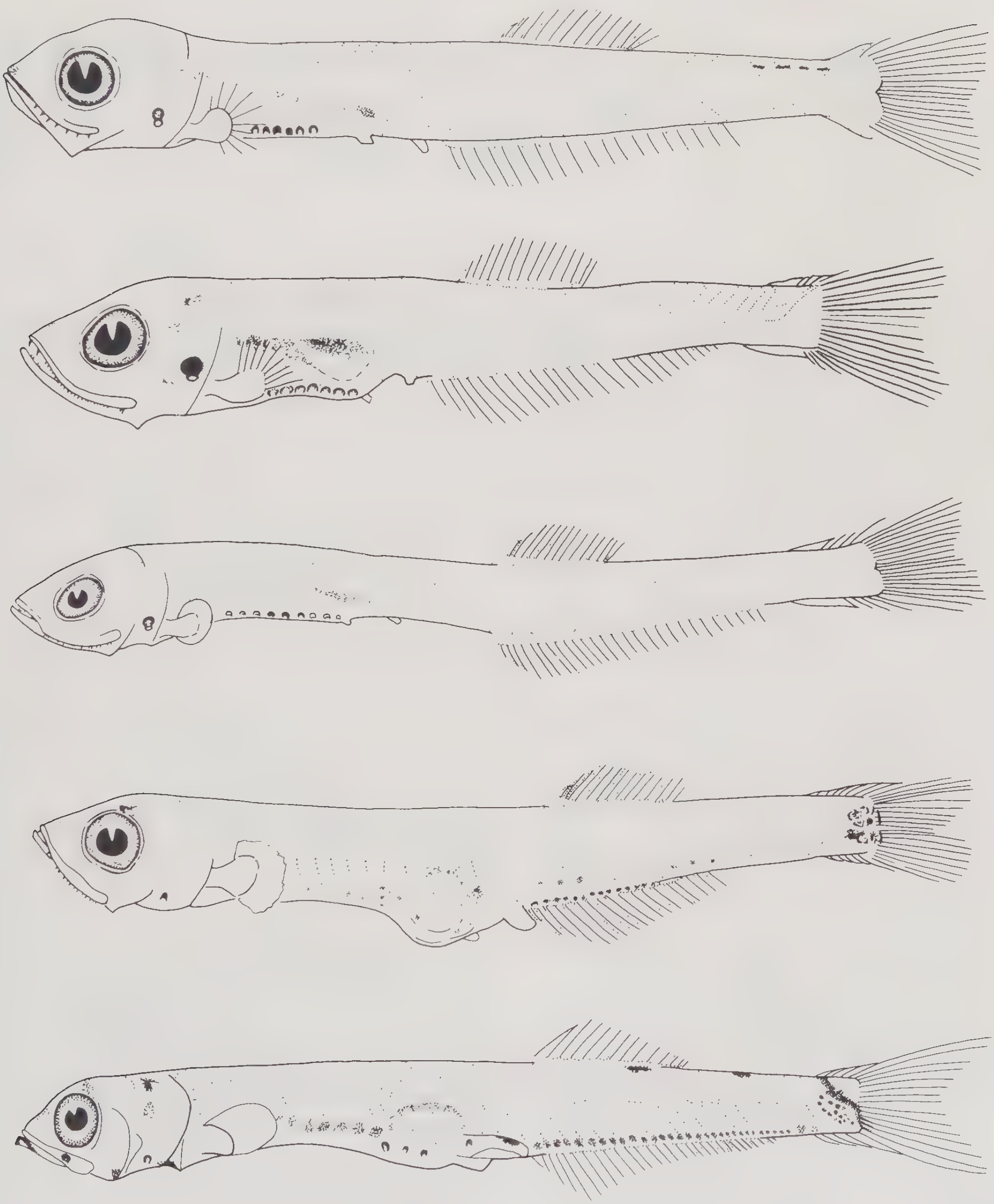


Fig. 101. Lateral view from top to bottom: *Gonostoma bathyphilum* 11.0 mm SL modified after Ahlstrom (1974); *Gonostoma elongatum* 9.8 mm SL modified after Ahlstrom (1974); *Gonostoma ebelingi* 15.0 mm SL modified after Ahlstrom (1974); *Gonostoma atlanticum* 12.0 mm SL modified after Ahlstrom (1974); *Gonostoma denudatum* 20.7 mm SL modified after Sanzo (1931d).

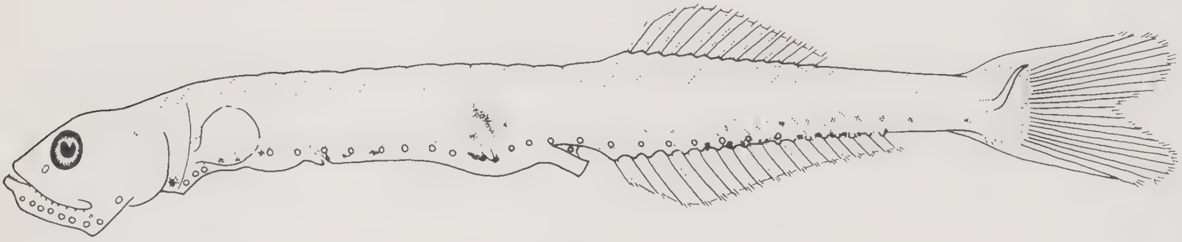


Fig. 102. *Cyclothone signata* 9.0 mm SL, drawn by H. Orr.

and Type Gamma, as being more specialized. This recognition, although not stated by these authors, is based on a concept that Types Alpha and Gamma photophores of some stomiiformes appear to be elaborations of Type Beta photophores. In other words, their particular features appear to be developmental terminal additions to Type Beta photophores and are therefore available for use as synapomorphies for stomiiform subgroups. Although more detailed analyses of these features are needed, for the sake of discussion we here accept that Type Beta photophores are primitive for stomiiforms.

Weitzman (1974:338), on the basis of outgroup comparison (not described or discussed in his text), considered four proximal pectoral-fin radials to be primitive for stomiiforms, their reduction to three or fewer to be specialized. We see no reason to change that analysis. Thus three or fewer proximal pectoral-fin radials are available as synapomorphous characters for stomiiform subgroups.

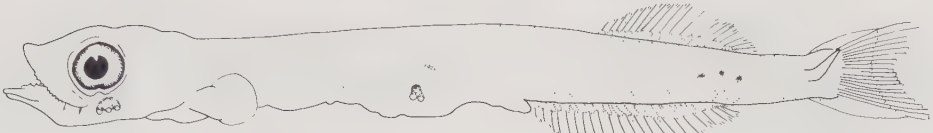
Ahlstrom (1974:660) described what can be labeled as "white" photophore development in which most, or at least the ventral series of photophores, are "laid down initially during a white photophore stage [before black pigment develops] and only a few photophores are late forming." One form or another of "white" photophore development is common to all stomiiforms except those including the gonostomatid genera *Bonapartia, Margrethia,* and *Gonostoma,* and the sternoptychids of Weitzman (1974). Members of these gonostomatid and sternoptychid genera have a protracted metamorphosis from the larval stage as well as a gradual, more extended photophore formation. This latter type of photophore development appears to be an elaboration of "white" photophore development and thus we consider white photophore development primitive with respect to the more complicated forms having prolonged photophore development. Again, much information of an anatomical and developmental nature remains to be gathered from the process of photophore development.

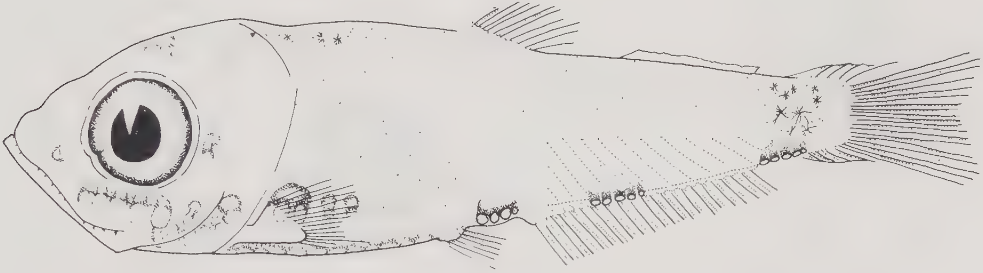
If "white" photophore development and Type Beta photophores are primitive in regard to stomiiform subgroups and therefore unavailable as synapomorphies for stomiiform subgroups, then the conflict regarding the distribution of characters among taxa between Ahlstrom (1974) and Weitzman (1974) disappears in a phylogenetic analysis by somewhat altering certain of the groups of both authors as follows.

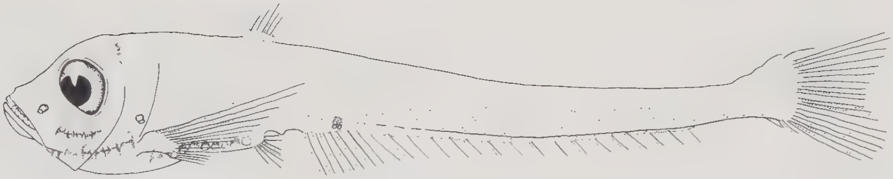
In our tentative scheme of relationships, Weitzman's Sternoptychidae and Ahlstrom's Group (2) genera (Ahlstrom, 1974: 671), *Bonapartia, Margrethia,* and *Gonostoma,* the Gonostomatidae in the strictest sense, are united by a synapomorphy consisting of a specialized form of prolonged metamorphosis and photophore development described by Ahlstrom (1974: 660–661). See also Tables 52–54 herein. These three gonostomatid genera and *Cyclothone* apparently share derived characters of the jaws and associated head parts which will be explained in a later contribution. These four genera retain the primitive Type Beta photophores, a character relating stomiiforms only at the ordinal level. In our opinion these four genera constitute the Gonostomatidae and *Cyclothone* may have lost prolonged photophore development through paedomorphic reversal associated with the small size of most of its members, a situation needing further study.

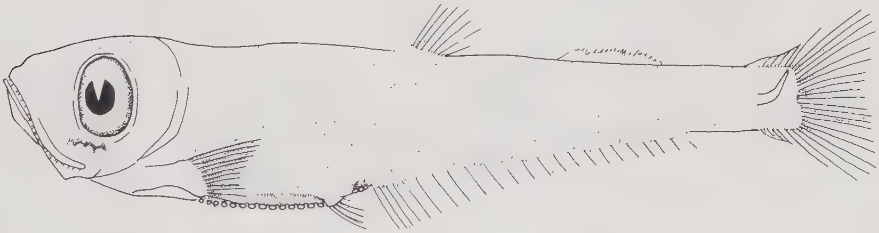
The Sternoptychidae have specialized Type Alpha photophores and the several other synapomorphies listed by Weitzman (1974:446–448). In addition they apparently share a unique photophore growth pattern previously unrecorded. One of us (Weitzman) has been studying photophore development in relation to phylogenetic studies in stomiiforms and has found that each cluster or group of photophores of the sternoptychids appears to develop by budding from one single photophore rather than by fusion at a later growth stage of separately developed photophores. This is a terminal developmental addition in photophore ontogeny and both outgroup comparison and developmental information indicate that this pattern of photophore formation is a specialization in comparison to the simpler appearance of single, separate body photophores (usually one per scale in any given series found in other stomiiforms). This growth character appears to be present in all sternoptychid genera for which we have developmental information. It is therefore a likely synapomorphy for the group.

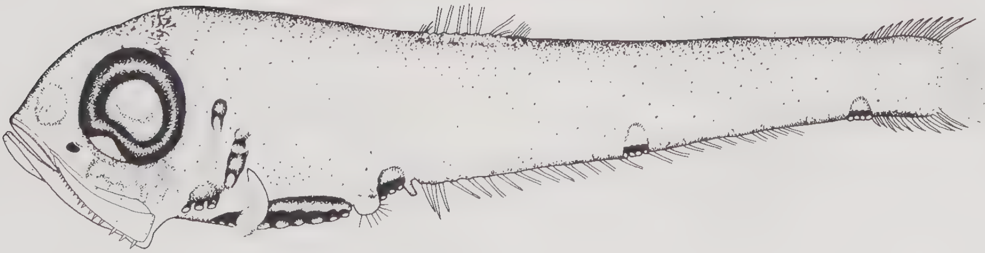
Manducus (based on the type species, *Gonostoma maderense* Johnson) is a primitive stomiiform, having ordinal-level characters with no known specialized characters except the absence of an adipose fin and a short neural spine on the preural centrum. The latter may be a primitive rather than a specialized stomiiform feature. *Diplophos* (based on the type species *Diplophos taenia* Günther) appears to have a transitional stage pectoral radial morphology between *Manducus* on the one hand and the Photichthyidae of Weitzman (1974) (an ill-defined group) and the Stomiidae on the other. In *Manducus* the cartilages and bones of proximal pectoral-fin radials III and IV remain separate whereas *Diplophos* has the cartilages, but not the bones, of the two elements fused, Fink and Weitzman (1982:65–67). In the "photichthyids" and stomiids the cartilages and bones of the two medial pectoral-fin radials are fused. This represents the terminal condition in the transition series except that in some genera there is a reversal of radial numbers and in *Eustomias* there occurs a further specialized, reduced pectoral-fin radial

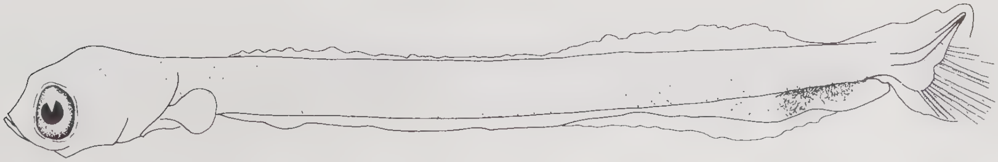












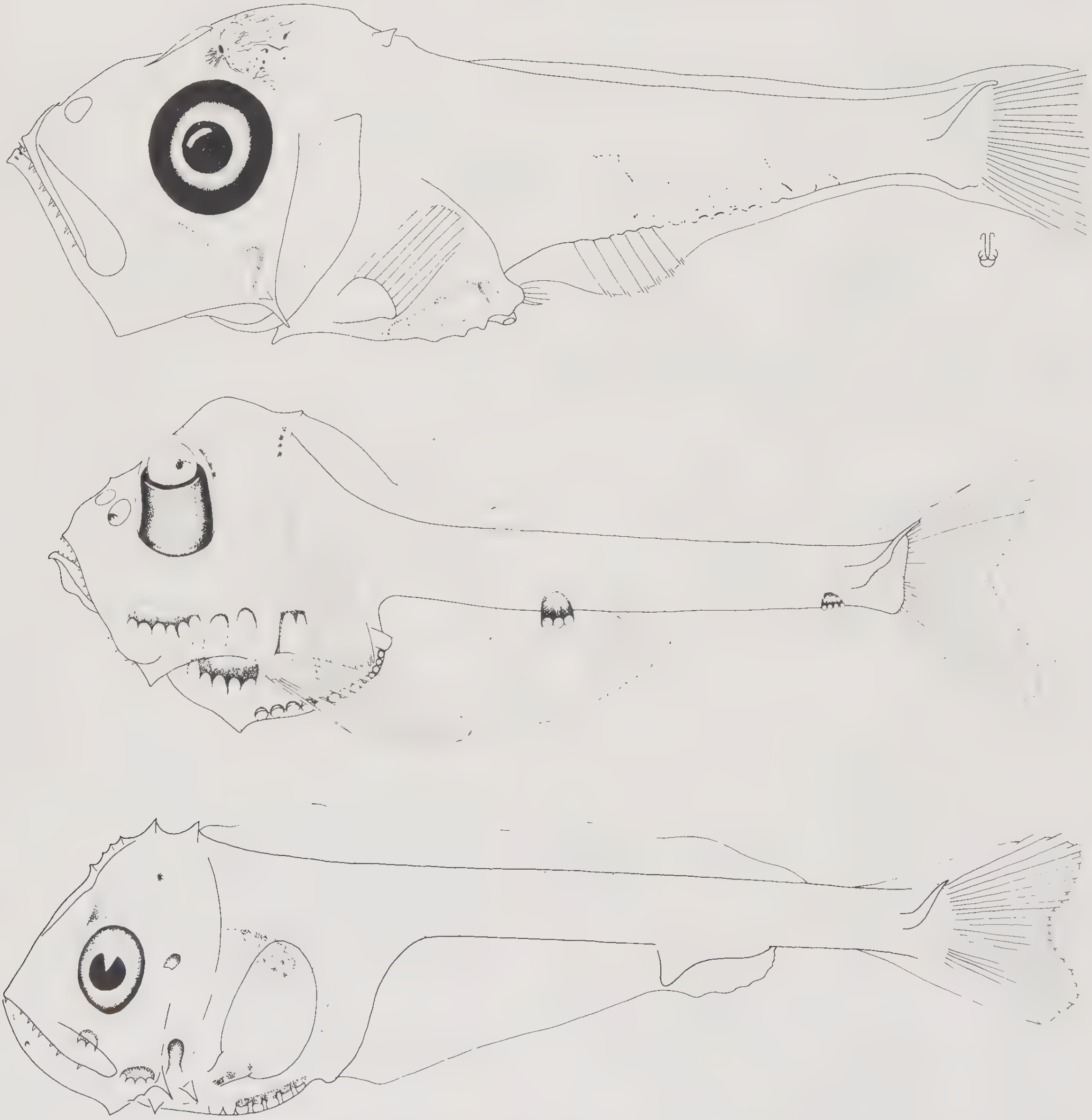


Fig. 104. Lateral views from top to bottom: *Polyipnus polli* 5.2 mm SL R/V GERONIMO Cr. 2, Sta. 155, 05°28′S, 01°120′E, August 21, 1963, drawn by J. C. Javech; *Argyropelecus hemigymnus* 7.8 mm SL modified after Sanzo (1931d); and *Sternoptyx* sp. 8.8 mm SL, drawn by H. C. Orr.

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Fig. 103. Lateral views from top to bottom: *Araiophos eastropas* 8.8 mm SL modified after Ahlstrom and Moser (1969); *Maurolicus muelleri* 10.8 mm SL modified after Ahlstrom (1974); *Danaphos oculatus* middle metamorphosis modified after Ahlstrom (1974); *Valenciennellus tripunctulatus* middle metamorphosis modified after Ahlstrom (1974); *Argyripnus atlanticus* 18.7 mm SL modified after Badcock and Merrett (1972); and maurolicine Alpha 7.5 mm SL modified after Ahlstrom (1974).

condition. The "photichthyids" and stomiids have specialized Type Gamma photophores, although it is not known that all genera in these groups have Type Gamma photophores; this is a problem for further investigation. *Manducus* and *Diplophos* retain Type Beta photophores and all of these fishes apparently retain "white" photophore development of one kind or another. These two characters are only useful at the ordinal level as synapomorphies. Again, further research on "white" photophore formation is needed since there appears to be more than one form of this development.

The monotypic *Triplophos* may or may not be related to *Manducus* and/or *Diplophos. Triplophos* has a variety of derived features not shared by *Manducus* or *Diplophos.* However, this tells us nothing about its possible relationships with these genera. *Triplophos* has four proximal pectoral-fin radials but with some reduction in radial IV, Type Beta photophores, and probably "white" photophore development, the last two characters synapomorphous only at the ordinal level. Four pectoral-fin radials are not a synapomorphy for stomiiforms at any level since the feature is found in most teleost outgroups. *Triplophos* appears to be a primitive stomiiform with certain autapomorphic features associated with an elongate body. Its relationships are uncertain and there may be indications in the head and pectoral girdle anatomy of a relationship with certain photichthyid genera. The problem needs much study.

Cyclothone retains Type Beta photophores and "white" photophore development but has its own specialized features such as only one pectoral-fin radial. It has a modified head and jaws, which resemble and are, in our opinion, synapomorphous with those of *Gonostoma.* The single pectoral-fin radial might be thought of as a terminal stage in a transition series from *Manducus* (with four pectoral-fin radials) to *Diplophos* to some members of the "Photichthyidae" and then to *Cyclothone.* However, *Cyclothone* does not have specialized Type Gamma photophores of the "photichthyid" genera. The phylogenetic relationships of *Cyclothone* may not be certain as yet, but in many respects it bears a resemblance to the three gonostomatid genera and we favor its placement with these genera. See also discussion above.

Although we have perhaps resolved the differences between Ahlstrom (1974) and Weitzman (1974), we have not achieved a useful phylogeny of most stomiiform groups. Rather, we have attempted to outline certain suggested hypotheses of relationships to be investigated in the future with additional data. Adult morphological data of the kind used by Weitzman to define and relate the sternoptychid genera are available in abundance and may be useful for other stomiiform groups. A closer look at growth stages with the specific purpose of looking for possible developmental specializations and terminal additions to characters found in outgroups should greatly aid in delineating relationships among the stomiiform genera. However, problems associated with a high percentage of homoplasy can be expected for some groups. The answers to problems of stomiiform interrelationships will not come easily.

Consideration of certain features is in order. For example, larvae of *Diplophos* superficially resemble those of *Chauliodus* with their prolonged development to a large larval size and great elongation with bodies that are circular in cross section. Are these convergent larval specializations or primitive stomiiform features found only in certain stomiiform genera? The ventral pigmentation on the body of developing *Diplophos* resembles that of developing paralepidids and myctophoids. Is this a primitive stomiiform feature of *Diplophos* shared with certain stomiiform outgroups or a gross convergence of pigment patterns?

Woodsia and *Ichthyococcus* share with certain stomiid genera (for example, *Eustomias*) such developmental features as elongate pectoral-fin rays, trailing guts, pigmentation patterns, and bodies with a circular cross section. Some, if not all, of these may be shared larval specializations. But again, independent appearance of these characters indicated by a high degree of homoplasy may be a vexing problem. Larvae of other genera such as *Vinciguerria, Pollichthys,* and *Cyclothone* have body shapes and certain other features that closely, but presumably superficially, resemble those of clupeoid larvae. Detailed comparisons of these similarities may possibly distinguish between homology and convergence among these taxa.

In summary, a future phylogenetic analysis based on much additional data may clear up many of the problems of stomiiform generic relationships. However, at present we are left with numerous phylogenetic problems and assignment of certain genera to family-level groups at this time would be misleading. The above analysis retains Weitzman's Sternoptychidae. It restricts the Gonostomatidae to the genera *Bonapartia, Margrethia,* and *Gonostoma,* and we recommend the inclusion of *Cyclothone.*

The other groups of non-stomiid stomiiforms remain unclear as to family relationships. We agree with Fink and Weitzman (1982) that *Manducus* and *Diplophos* are primitive stomiiforms, but we cannot provide a stable classification for *Manducus, Diplophos,* and *Triplophos. Manducus* and *Diplophos* might seem to be sister taxa because of their similarity of appearance. However, they share no known specialized character or characters that would unite them as a stomiiform subgroup except the absence of an adipose fin and possibly a short neural spine on the preural centrum. Currently all their other shared characters seem primitive for stomiiforms. Further analysis of this situation is needed.

Triplophos is again very much like a primitive stomiiform in its head especially, but it has a number of specialized stomiiform features as listed by Grey (1964:106) and may show some relationship to some of the "photichthyid" genera.

That the genera classified in the "Photichthyidae" by Weitzman (1974) form some kind of related group seems reasonable. However, relationships among these genera are not known. That these "photichthyid" genera are related to *Diplophos* is possible, and that the stomiids are related to the "photichthyids" is, in our view, very probable. The larval specializations of *Woodsia* and *Ichthyococcus* noted above, may be important here because they may be synapomorphies relating these genera to the stomiids.

Until the developmental and adult morphological features of many stomiiform genera are analyzed in detail, certain aspects of their developmental stages outlined, and detailed outgroup analysis performed on all putatively useful characters, we can make no certain predictions about relationships and classification.

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Resumption of Nursing in "Weaned" Hawaiian Monk Seal Pups

Doris J. Alcorn and John R. Henderson

It is not uncommon for Hawaiian monk seal *(Monachus schauinslandi)* pups to be nursed by mothers other than their own, and a mother may nurse two pups simultaneously (Johnson and Johnson 1978, 1981). Weaning by monk seal pups is determined to have occurred when the mother, usually emaciated from having nursed a pup for approximately five weeks without herself feeding, leaves her pup and swims to sea to feed.

However, pups already weaned from their natural mother have not been heretofore reported to resume suckling on another mother. During the spring of 1982 two such incidents were observed in the Northwestern Hawaiian Islands, one on Lisianski Island, and the other on neighboring Laysan Island. The former incident lasted only a few days, but the latter extended for an entire additional nursing period.

LISIANSKI ISLAND

At Lisianski Island in March 1982, one of us (JRH) observed a weaned male pup resumed suckling on a foster mother two days after the pup's weaning. The weaning had appeared normal, and after the mother returned from the sea, she was regularly seen the remainder of the field season. This pup had been weaned within 25 meters of its future foster mother on the same day that the foster mother pupped. For two days the female repeatedly rebuffed the weaned pup's attempts to suckle, but then acquiesced, and nursed it along with her own pup for two days.

The initial nursing period of the weened pup is not known, but it may have been considerably less than normal, as the pup was somewhat underweight and had completed only 10% of its pup molt, which is normally finished prior to weaning.

LAYSAN ISLAND

On 18 March 1982, one of us (DJA) observed a female pup during the first 1982 Laysan Island seal census. The pup was with an adult female, and was estimated to be at least two weeks old based on its black pelage and size. Thereafter, the mother-pup pair was observed daily (with the exception of two days) until the pup was weaned on 6 April. The size of the pup was normal at weaning, thus supporting the initial age estimate. The first nursing period for this pup was therefore estimated at a minimum of 33 days.

This weaned Laysan pup appeared to actively search for a mother for 7-8 days before it was adopted by an adult female whose pup had died. The weaned pup was then nursed by its foster mother for 34-45 days. The rest of this section describes the adoption, second nursing period, and second weaning of this pup.

The pup stayed at the first weaning site for three days, then moved west approximately 85 meters. At that time it was following an adult female who had temporarily lost her pup during a pup exchange. The weaned pup stayed within 1.5 meters of this female and even rested against her once, although she ignored the weaned pup and vocalized loudly. The next afternoon the female and her pup were observed to be reunited, but the weaned pup continued to follow the mother-pup pair and remained close to them for the next two days.

On 12 April the weaned pup was observed near a mother with a dead pup. The death had occurred during birth on 11 April (p.m.) or 12 April (a.m.) On 13 April the dead pup was removed for a necropsy while the mother was asleep. When the mother awoke, she vocalized while looking around, then moved toward the area of the weaned pup. Later that afternoon the mother of the dead pup was seen 18 meters east of the death site, following the weaned pup. They were together on 14 April, and on 15 April was observed.

To verify that the "weaned" pup was still with its foster mother and was suckling, observations were made daily between 15 April and 18 May., with the exception of four days. Although extensive observations were not made, the nursing activity appeared normal; the longest single nursing bout recorded was 21 min on 28 April.

The last verified nursing bout was on 17 May. The second nursing period was therefore at least 34 days, and probably extended the entire 35 days the pup and foster mother were seen together. This makes the combined number of days the pup was nursed by both mothers an estimated 67-68 days, which is about

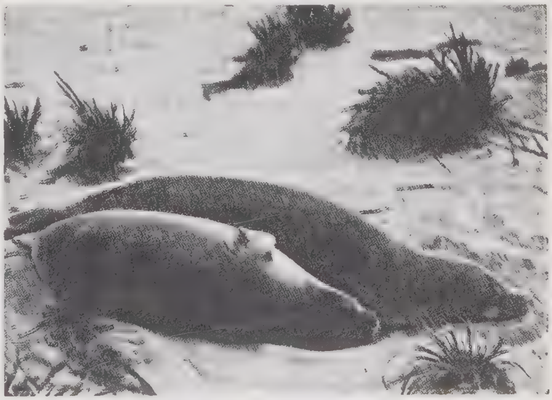

Fig. 1. Laysan pup with foster mother; after 53 days of nursing by a natural mother, and then a foster mother, the pup was unusually large.

Photo by D. Alcorn

twice the average nursing period of 35-36 days, and much longer than the range of 27-50 days reported for monk seals on Laysan (Johnson and Johnson 1978, 1981).

This pup was moderately long a second weaning, measuring roughly 138 centimeters from nose to tail tip. However, it mainly differed from the other newly weaned pups in its immense girth (Fig. 1). When last seen on 29 June before the Laysan research camp was terminated, it was still unusually fat.

CONCLUSIONS

These two cases are unique because the pups had already been weaned before being nursed by another mother. The Laysan occurrence is of special interest because of the combined length of the nursing periods.

Several factors probably contributed to the initiation and duration of the Laysan event: (1) The pup was persistent in attempting to locate a new mother after it was first weaned; (2) it was in the right place at the right time; i.e., near a mother who had lost a pup, and (3) it did not become aggressive towards the female nursing it, unlike some Laysan pups approaching weaning age. It it not known whether the foster mother would have adopted this weaned pup if her own dead pup had not been removed for necropsy. However, the observation at Lisianski of temporary nursing of a weaned pup by a female whose own pup was alive indicates that females do accept such pups despite the presence of the natural pup.

The fact that a nursing Hawaiian monk seal will accept a pup other than its own may have adaptive advantages. The greater fat reserves gained by the adopted Laysan pup due to extra nursing gave it an advantage in surviving the long weaning period when pups live off fat reserves while learning to catch prey. Older age at final weaning meant the pup was protected by an adult female for a extended period of time, and was more experienced, thus perhaps better able to cope with sharks, advances of adult males, or other hazards of the postweaning period. The extra two days' nursing by the Lisianski pup may have helped compensate for what was possibly an abnormally short nursing period.

There were no obvious disadvantages in these two adoption cases. However, in general it could be disadvantageous to a foster mother's natural pup if it were abandoned or received less nourishment because of a foster pup.

ACKNOWLEDGEMENTS

We wish to thank Dr. C. Whittow, Dr. Kenyon, and E. Kridler for their comments on the manuscript.

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ERRATUM

The Editors apologize for the errors which appeared in Doris J. Alcorn and John R. Henderson's paper entitled "Resumption of Nursing in 'Weaned' Hawaiian Monk Seal Pups". The paper appeared in the August 1984 issue of *'Elepaio* (Vol. 45, No. 2).

On page 11 of the August 1984 issue, after the 5th paragraph under the Laysan Island section, a paragraph was inadvertently omitted The missing paragraph follows:

"The second weaning occurred during the night of 18 May; at 0649 hr, 19 May, the pup was seen alone in the water. The weaning appeared to be normal, and was not due to mortality of the foster mother, as she was resighted on 25 May."

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SPAWNING FREQUENCY AND SEX RATIO IN THE PERUVIAN ANCHOVY, *ENGRAULIS RINGENS*[1]

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ABSTRACT

Spawning frequency was determined for the first time for the Peruvian anchovy, *Engraulis ringens*, using the incidence of postovulatory follicles. The agreement between two independent frequency estimates, one for females taken one day after spawning and another for females taken two days after spawning, demonstrated the reliability of this method. In August-September, the main period of annual spawning, 16.04% of the female population of the central and northern anchovy stock off Peru spawned per day: i.e., every 6.23 days the average female spawned a new batch of eggs. Hydration of ovaries began as early as 0700 hours in the morning. Spawning occurred at night between 1800 and 0200 hours, reaching a maximum at about 2200 hours. Sex ratio was 57.9% females by weight. The vulnerability of females to the purse seine changed with their reproductive state. Females with hydrated ovaries who were ready to spawn seemed to attract males and to form male-dominated ''spawning schools'' by segregating from ''normal'' schools at night.

RESUMEN

La frecuencia de puesta en la anchoveta peruana *Engraulis ringens* ha sido determinada por primera vez, tomando como base la incidencia de folículos post-ovulatorios. La concordancia entre dos estimaciones independientes de esta frecuencia, obtenidas de hembras un y dos días después de la puesta, demuestran la fiabilidad de esta método. Anualmente, el período principal de la puesta abarca de Agosto a Septiembre, cuando la puesta diaria comprendió el 16.04% de las hembras de las poblaciones del norte y centro de la región peruana; es decir, cada 6.23 días una hembra promedio pone una nueva remesa de huevos. La hidratación de los ovarios se inició temprano, a eso de las 0700 de la mañana. La puesta se produjo entre las 1800 y 0200 horas, alcanzando un máximo a las 2200 horas aproximadamente.

La proporción de sexos calculada en peso fue de 57.9% de hembras. La vulnerabilidad de las hembras a la pesca con redes de jareta varía con la fase reproductora enque se encuentran. Hembras con ovarios hidratados, que estaban dispuestas para la puesta parecian atraer a los machos y formar cardúmenes de puesta dominados por machos separándose de los cardúmenes normales durante la noche.

INTRODUCTION

In the past, estimating the spawning biomass of multiple-spawning pelagic fish species like anchovies and sardines posed serious problems because no adequate methods were available to determine the spawning frequency, i.e., the fraction of the female population spawning per unit time. Recently, Hunter and Goldberg (1980) solved this problem for the northern anchovy, *Engraulis mordax*, by an ingenious technique. They followed up the suggestion of Yamamoto and Yoshioka (1964) that spawning frequency could be determined by incidence of postovulatory follicles—the remnants of ovulated follicles.

Follicles are the layers of cells surrounding developing oocytes in the ovaries. After ovulation, they immediately begin to deteriorate and are then called postovulatory follicles (Hunter and Goldberg 1980). Hunter and Goldberg identified postovulatory follicles in histological sections of northern anchovy ovaries and classified the females into three groups: those spawning on the night of capture (new, or day-0 postovulatory follicles), those spawning on the night previous to capture (day-1 postovulatory follicles), and those showing no evidence of recent spawning. Hunter and Goldberg then used the frequency of day-1 postovulatory follicles as a measure of spawning frequency. They used anchovy spawned in the laboratory to develop this technique (Leong 1971). Because the time of induced spawning was known, they could de-

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[1] Publication No. 15 of the ''Cooperative Peruvian-German Fisheries Research Project'' (PROCOPA)

[Manuscript received April 3, 1984.]

scribe histological criteria for aging postovulatory follicles. These criteria were then applied to field populations.

Hunter and Goldberg collected their field samples with a small trawler, which could catch adult anchovy only at night. They were therefore not able to obtain complete 24-hour time series of females with postovulatory follicles. This could have resulted in a bias in the estimation of spawning frequency, since Hunter and Goldberg (1980) had already shown that females captured on the night of spawning were oversampled.

It is well known that prior to ovulation the ovaries of teleost fish take up fluid, a process called hydration (Fulton 1898). Hunter and Macewicz (1980) suggested that if anchovies could be sampled during the day, it might be possible to use the incidence of females with hydrated ovaries ("hydrated females") to determine spawning frequency. The advantage would be that time and money could be saved because histological examination would no longer be required.

In this paper we estimate the spawning frequency of the Peruvian anchovy, *Engraulis ringens*, using Hunter and Goldberg's (1980) method. We can answer some of the questions posed by Hunter and Goldberg and Hunter and Macewicz (1980) because we used a different technique to sample anchovy. In Peru, anchovy were collected with a purse seiner and could therefore be sampled in the day as well as at night. Thus, females with postovulatory follicles and females in the hydrated, prespawning stage could be obtained for an entire 24-hour cycle. Any time-related bias in the incidence of females with postovulatory follicles would become obvious when a series of samples taken at regular intervals over 24 hours was examined. Thus, the use of a purse seine for the Peruvian anchovy gave new insights into bias in estimating spawning frequency. Because hydrated females were sampled during the day, the alternative approach of using incidence of hydrated females to estimate spawning frequency could also be evaluated. Thus the objectives of this paper are to evaluate Hunter and Goldberg's (1980) method for estimating spawning frequency by using a 24-hour sampling scheme and to determine the effect of different sampling gear (trawl versus purse seine) on the estimates of spawning frequency and sex ratio of Peruvian anchovy schools.

The findings of Hunter and Goldberg (1980) enabled the Southwest Fisheries Center, La Jolla, to develop the "egg production method" (Parker 1980; Stauffer and Picquelle 1980) for estimating spawning biomass of the northern anchovy off California. Two of the five parameters required for this method are spawning frequency and sex ratio. The data presented here were used to estimate the spawning biomass of the Peruvian anchovy using the egg production method (Santander et al., in press).

METHODS

Adult anchovies were collected with a purse seiner. The cruise was run from August 25 to September 17, 1981. It began in the south and proceeded northwards. The purse seine stations were usually located within 20 miles of the shore because of adverse weather conditions and the scarcity of anchovy schools farther offshore. Most of the collections came from the southern part of the investigation area because weather conditions in the north prohibited use of the purse seine (Figure 1). The total number of collections was 49.

Immediately after capture, the anchovy's body cavity was opened from the anus to the ventral fins. Only live specimens were processed because of the rapid degeneration of the postovulatory follicles. The fish were preserved in a 4% buffered formaldehyde solution. Seawater was not used to dilute the formaldehyde solution because it causes a white precipitate that makes reading the histological sections difficult.

Twenty mature females were collected at random

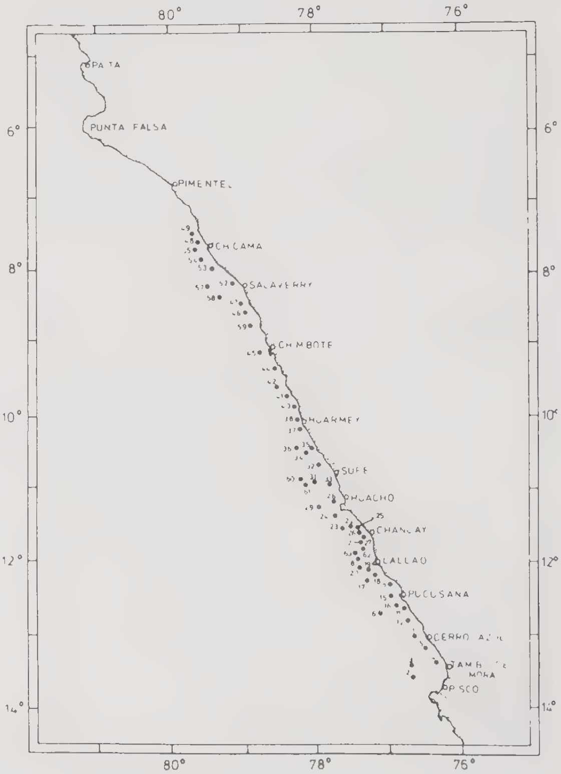

Figure 1. Map of surveyed area and location of samples of anchovies.

for histological analysis. Standard methods were used to process the ovaries. A small cube of about 0.125 cm^3 was cut from the center of the ovary. It was dehydrated in a series of alcohol solutions and embedded in paraplast. The histological sections were cut at 6 µm and stained with hematoxylin/eosin. A detailed account of the procedure is given in Alarcón et al. (in press). The criteria developed by Hunter and Goldberg (1980) for aging postovulatory follicles are based on the stages of degeneration through which they pass. Because postovulatory follicles degenerate rapidly, their age can only be determined up to 50 hours after spawning. The age classes for postovulatory follicles used here are somewhat different from those described by Hunter and Goldberg (1980).

The fraction of females (sex ratio) was estimated for each collection from a subsample consisting of the first 800 g of fish. The total body weight was used, because the gonad-free weight of males was not measured. The total body weight of hydrated females was adjusted (Santander et al., in press) for the excess weight of the hydrated ovary (Stauffer and Picquelle 1980). Immature fish were included because it was not possible to distinguish between mature and immature males. In order to attain exactly 800 g of fish it was necessary to use only that fraction of the weight of the last fish in the collection that completed the 800 g. Sample mean and variance were estimated according to Stauffer and Picquelle (1980):

$$\bar{\bar{R}} = \frac{\Sigma \bar{R}_i}{n}$$

and

$$V(\bar{\bar{R}}) = \frac{\Sigma(\bar{R}_i - \bar{\bar{R}})^2}{n(n-1)}$$

where

$\bar{R}_i$ = fraction of females by weight in percent in collection i
$\bar{\bar{R}}$ = average fraction of females by weight in percent from all collections.

For estimating the spawning frequency (fraction of mature females spawning per day) we used only postovulatory females taken at least 9 hours after peak spawning (2200 hours), to prevent bias arising from sampling females during the time of day when they are actually spawning. Two independent 24-hour sets of postovulatory follicles could be separated: one set of postovulatory follicles with an age between 9 and 32 hours after spawning and another set of postovulatory follicles with an age between 33 and 56 hours. Henceforth females with ovaries containing postovulatory follicles of 9-32 hours will be called day-1 females; those having ovaries containing postovulatory follicles of 33-56 hours will be called day-2 females.

Assuming that sampling of females with hydrated ovaries, day-1 females, or day-2 females is unbiased, then the spawning fraction for collection i is estimated by:

$$F_i = \frac{m_{hi}}{m_i} \text{ or } \frac{m_{1i}}{m_i} \text{ or } \frac{m_{2i}}{m_i}$$

where

$$m_i = m_{hi} + m_{1i} + m_{2i} + m_{ai}$$

and where

m_{hi} = number of hydrated females in collection i
m_{1i} = number of day-1 females in collection i
m_{2i} = number of day-2 females in collection i
m_{ai} = number of females that have not spawned within the past 9 to 56 hours (includes females with postovulatory follicles of an age of less than 9 hours)
m_i = number of mature females in collection i
F_i = spawning fraction in collection i

The results for the Peruvian anchovy were similar to results for the northern anchovy (Stauffer and Picquelle 1980); they indicated that hydrated females were oversampled. To correct for this apparent oversampling, under the assumption that the true fraction of hydrated females is the same as the fraction of day-1 or day-2 females, m_{hi} is replaced by $\frac{m_{1i} + m_{2i}}{2}$ such that

$$\hat{F}_i = \frac{m_{1i}}{\frac{m_{1i} + m_{2i}}{2} + m_{1i} + m_{2i} + m_{ai}}$$

$$\text{or } \frac{m_{2i}}{\frac{m_{1i} + m_{2i}}{2} + m_{1i} + m_{2i} + m_{ai}}$$

where

$\hat{F}_i$ = corrected fraction of day-1 or day-2 females in collection i.

The estimates for mean and variance are given by:

$$\bar{F} = \frac{\Sigma\, m_{1i} + m_{2i}}{2\sum \frac{m_{1i} + m_{2i}}{2} + m_{1i} + m_{2i} + m_{ai}} = \frac{\Sigma\, m_{1i} + m_{2i}}{2\, \Sigma\, m_{yi}}$$

and

$$V_{(\bar{F})} = \frac{1}{n(n-1)} \sum \left(\frac{m_{yi}}{\bar{m}}\right)^2 (\hat{F}_i - \bar{F})^2$$

where

$\bar{F}$ = average fraction of females spawning per day from all collections

$m_{vi} = \dfrac{m_{1i} + m_{2i}}{2} + m_{1i} + m_{2i} + m_{ai}$ = corrected number of mature females in collection i

$\bar{m}$ = average number of mature females corrected per collection i

$$= \frac{\sum m_{vi}}{n}$$

n = number of collections.

RESULTS

Peak Spawning Time

To age postovulatory follicles, one must determine the duration of the daily spawning period and its midpoint. This goal can be reached in three ways: (1) by recording time of incidence and frequencies of new postovulatory follicles from samples of adult anchovy females; (2) by recording the decline of occurrence of hydrated females; and (3) by recording time of occurrence and frequencies of newly spawned eggs from ichthyoplankton samples. Hunter and Macewicz (1980) demonstrated clearly that the percentage of northern anchovy females with hydrated oocytes declined steadily from 10% to 14% at 1800 hours to 0% at 2400 hours, and concluded that 2200 to 2300 hours was the period of maximum spawning.

The data from the Peruvian anchovy did not provide as clear a picture, for two reasons. Hunter and Macewicz (1980) collected all their samples at night between 1800 and 0500 hours, whereas only 40% of the Peruvian samples were collected between 1800 and 2300 hours, and only one sample was obtained between 2300 and 0700 hours. In the Peruvian samples, females with new postovulatory follicles were recorded for the first time at 1800 hours, but their numbers were very low (Table 1). The numbers of females with hydrated oocytes ranged between 7.5% and 51.7% from 0700 to 2030 hours and declined sharply to 3.3% and 5% at 2130 to 2230 hours, respectively (Figure 2). The best data for estimating the midpoint of the nightly spawning period was that provided by the ichthyoplankton survey. The occurrence of newly spawned eggs in the water column demonstrated that peak spawning time of the Peruvian anchovy is between 2200 and 2300 hours (Santander et al., in press).

Combining all these data leads to the conclusion that Peruvian anchovy spawning starts at sunset, around 1800 hours, and that the period of maximum spawning is between 2200 and 2300 hours. It was not possible to estimate the time when nightly spawning ceases, but by analogy to the northern anchovy, spawning probably ceases around 0200 hours. For convenience, 2200 hours is taken as the midpoint of the daily spawning period in the following analysis.

TABLE 1
Collections Containing Female Peruvian Anchovy with New Postovulatory Follicles

Collection no.	Time of day	No. of new postovulatory follicles
46	1800	1
4	1930	1
12	1930	2
41	2015	1
25	2100	1
21	2230	2
1	0315	1

Spawning Frequency

The spawning frequency is the fraction of mature females that spawns per day. In theory, one should get three independent estimates of this parameter: (1) the percentage of females with hydrated oocytes, (2) the percentage of females with day-1 postovulatory follicles, and (3) the percentage of females with day-2 postovulatory follicles. Because females with hydrated oocytes tend to be oversampled, they cannot be used for this purpose. The age of postovulatory follicles can only be determined up to about 50 hours after spawning, because older postovulatory follicles may be confused with other structures, such as atretic follicles (Hunter and Goldberg 1980; Hunter and Macewicz 1980).

Because the northern anchovy were sampled only at night (Hunter and Goldberg 1980; Hunter and Mace-

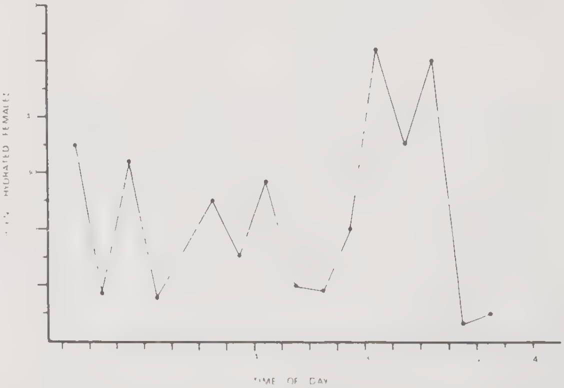

Figure 2. Change of percentage of hydrated females in collections with time of day

wicz 1980; Stauffer and Picquelle 1980), investigators could use only day-1 postovulatory follicles to estimate spawning frequency. Our use of a purse seiner for sampling the Peruvian anchovy permitted collection of samples at any time of day. Consequently, we obtained two independent sets of data for estimating spawning frequency (day-1 and day-2 females) and compared them.

The way in which these two sets of data were obtained is demonstrated in Table 2. It was assumed that all anchovy females spawn at 2200 hours. Because the earliest sample was collected at 0700 hours, we considered that time the beginning of the day-1 and the day-2 periods. Postovulatory follicles found at this time are, according to their structure, assigned to one of the following three groups: day-1, day-2, or older postovulatory follicles. They are given ages of 9, 33, or more than 56 hours, respectively. Table 3 contains the summary of all data: (1) date and time of each collection, (2) numbers of hydrated, day-1, and day-2 females, (3) hours past spawning of each collection, (4) values corrected for oversampling hydrated females, and (5) percentage of hydrated, day-1, and day-2 females per collection.

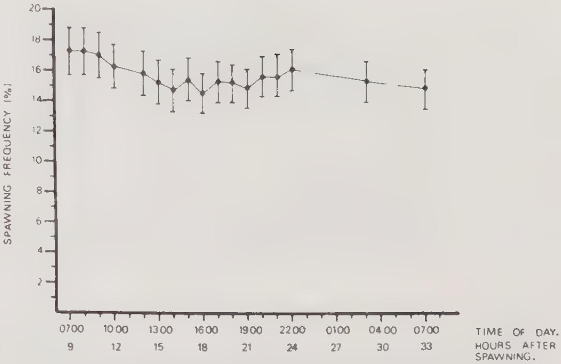

Figure 3. Spawning frequencies calculated from consecutive 24-hour periods. The time of day indicates at what time each 24-hour period begins. The corresponding hours after mean spawning time (2200 hours) are also indicated. Standard deviations are added.

Stauffer and Picquelle (1980) suggested that females with new postovulatory follicles may also be oversampled, but lacked data with which to test this hypothesis. To test it, we calculated the mean spawning frequencies for consecutive 24-hour periods. First, we calculated the mean spawning frequency for the first 24-hour period starting at 0700 hours—9 hours after mean spawning time. Only postovulatory follicles within the age range from 9 to 32 hours were included (Figure 3). Then we calculated the spawning frequency for the second 24-hour period, beginning at 0800 hours and including postovulatory follicles with

TABLE 2

Time of Collection of Females and the Age of Postovulatory Follicles

	Time of day	Age of postovulatory follicles (hours past spawning)	
		Day-1	Day-2
Night of spawning	22.00 (Peak spawning)		
1st day following spawning	07 00-07.59	9	33
	08.00-08.59	10	34
	09.00-09.59	11	35
	10.00-10.59	12	36
	11.00-11.59	13	37
	12.00-12.59	14	38
	13.00-13.59	15	39
	14.00-14.59	16	40
	15.00-15.59	17	41
	16.00-16.59	18	42
	17.00-17.59	19	43
	18.00-18.59	20	44
	19.00-19.59	21	45
	20.00-20.59	22	46
	21.00-21.59	23	47
	22.00-22.59	24	48
	23.00-23.59	25	49
2nd day following spawning	00.00-00.59	26	50
	01.00-01.59	27	51
	02.00-02.59	28	52
	03.00-03.59	29	53
	04.00-04.59	30	54
	05.00-05.59	31	55
	06.00-06.59	32	56

an age from 10 to 33 hours. We repeated these calculations for a total interval of 48 hours, always advancing by one hour, so that the last 24-hour period starts again at 0700 hours—33 hours after mean spawning time and includes postovulatory follicles with an age from 33 to 56 hours. Theoretically, there should have been 25 different 24-hour periods. However, because no collections were taken at 1100 hours and only one between midnight and 0700 hours (Table 3), only 17 consecutive 24-hour periods are included in Figure 3. The spawning frequencies calculated from these 17 consecutive 24-hour periods showed no strong trend over the observed 48-hour interval, and ranged from 14.70% to 17.26%. We conclude that females with postovulatory follicles of 9 hours and older are equally available to the purse seine.

If spawning frequency data for day-1 females and for day-2 females are independent of each other and identically distributed, they could be combined. Their combined total would double the sample size and

TABLE 3
Data Summary

				Hydrated females		Day-1 females		Day-2 females					$\hat{F}_1$	$\hat{F}_2$
Time of day	Collection No.	Date	Sex ratio (% females)	No. (m_{hi})	%	Hours past spawning	No. (m_{1i})	Hours past spawning	No. (m_{2i})	$\frac{m_{1i}+m_{2i}}{2}$	m_{ai}	m_{yi}	Day-1 (m_{1i}/m_{yi})	Day-2 (m_{2i}/m_{yi})
07.15	28	5.9.	52.76	11	55	9	0	33	0	0	9	9.0	0	0
07.25	38	8.9.	55.30	3	15	9	3	33	3	3.0	11	20.0	.1500	.1500
08.00	33	6.9.	83.01	0	0	10	2	34	1	1.5	17	21.5	.0930	.0465
08.30	26	2.9.	68.74	0	0	10	2	34	4	3.0	14	23.0	.0870	.1739
08.45	48	12.9.	45.32	5	25	10	6	34	3	4.5	6	19.5	.3077	.1538
09.00	5	26.8.	44.96	11	55	11	2	35	1	1.5	6	10.5	.1905	.0952
09.00	10	28.8.	31.51	7	35	11	6	35	1	3.5	6	16.5	.3636	.0606
09.00	42	9.9.	33.38	2	10	11	0	35	0	0	18	18.0	0	0
09.15	29	5.9.	90.50	2	10	11	2	35	3	2.5	13	20.5	.0976	.1463
09.30	17	30.8.	54.44	10	50	11	2	35	0	1.0	8	11.0	.1818	0
10.00	22	1.9.	67.33	0	0	12	2	36	1	1.5	17	21.5	.0930	.0465
10.10	52	16.9.	45.80	3	15	12	6	36	3	4.5	8	21.5	.2791	.1395
12.00	2	25.8.	68.95	2	10	14	5	38	3	4.0	10	22.0	.2273	.1364
12.00	57	17.9.	63.62	2	10	14	6	38	5	5.5	7	23.5	.2553	.2128
12.10	34	7.9.	70.96	10	50	14	3	38	0	1.5	7	11.5	.2609	0
12.30	27	2.9.	49.89	6	30	14	1	38	2	1.5	11	15.5	.0645	.1290
13.00	18	30.8.	55.32	3	15	15	2	39	2	2.0	13	19.0	.1053	.1053
13.10	53	16.9.	62.04	4	20	15	6	39	3	4.5	7	20.5	.2927	.1463
13.15	49	12.9.	59.29	2	10	15	4	39	2	3.0	12	21.0	.1905	.0952
14.15	11	28.8.	47.43	3	15	16	4	40	4	4.0	9	21.0	.1905	.1905
14.15	58	17.9.	28.18	11	55	16	1	40	1	1.0	7	10.0	.1000	.1000
14.45	35	7.9.	70.51	3	15	16	0	40	6	3.0	11	20.0	0	.3000
15.30	6	28.8.	81.27	2	10	17	9	41	1	5.0	8	23.0	.3913	.0435
16.00	15	29.8.	32.57	5	25	18	1	42	3	2.0	11	17.0	.0588	.1765
16.10	40	8.9.	60.38	1	5	18	3	42	5	4.0	11	23.0	.1304	.2174
16.15	20	31.8.	26.36	3	15	18	4	42	6	5.0	7	22.0	.1818	.2727
16.30	3	25.8.	74.42	0	0	18	4	42	7	5.5	9	25.5	.1569	.2745
16.45	23	1.9.	78.73	0	0	18	6	42	4	5.0	10	25.0	.2400	.1600
17.10	44	9.9.	62.12	2	10	19	1	43	3	2.0	14	20.0	.0500	.1500
17.35	54	16.9.	71.94	6	30	19	7	43	4	5.5	3	19.5	.3590	.2051
18.00	8	27.8.	45.21	1	5	20	1	44	1	1.0	17	20.0	.0500	.0500
18.00	36	7.9.	36.11	13	65	20	2	44	4	3.0	1	10.0	.2000	.4000
18.00	46	11.9.	29.90	16	80	20	1	44	0	0.5	3	4.5	.2222	0
18.15	31	5.9.	67.15	2	10	20	5	44	1	3.0	12	21.0	.2381	.0476
19.00	24	1.9.	60.38	3	15	21	1	45	2	1.5	14	18.5	.0541	.1081
19.15	19	30.8.	46.13	4	20	21	4	45	7	5.5	5	21.5	.1860	.3256
19.30	4	25.8.	55.33	13	65	21	3	45	0	1.5	4	8.5	.3529	0
19.30	7	26.8.	58.28	2	10	21	2	45	4	3.0	12	21.0	.0952	.1905
19.30	12	28.8.	12.62	17	85	21	0	45	0	0	3	3.0	0	0
19.30	16	29.8.	43.93	8	40	21	3	45	3	3.0	6	15.0	.2000	.2000
19.40	55	16.9.	65.52	2	10	21	1	45	5	3.0	12	21.0	.0476	.2381
20.10	45	9.9.	73.93	1	5	22	5	46	6	5.5	8	24.5	.2041	.2449
20.15	41	8.9.	15.86	19	95	22	0	46	0	0	1	1.0	0	0
21.00	25	2.9.	78.68	2	10	23	4	47	7	5.5	7	23.5	.1702	.2979
21.00	47	11.9.	79.20	0	0	23	4	47	4	4.0	12	24.0	.1667	.1667
21.15	32	5.9.	64.18	0	0	23	2	47	2	2.0	16	22.0	.0909	.0909
22.30	21	31.8.	79.68	1	5	24	3	48	4	3.5	12	22.5	.1333	.1778
22.55	37	7.9.	64.36	1	5	24	9	48	1	5.0	9	24.0	.3750	.0417
03.15	1	25.8.	51.42	2	10	29	5	53	1	3.0	12	21.0	.2381	.0476

TABLE 4

Arithmetic Means and Probability Values *p* and *q* of the Binomial Distributions of Hydrated, Day-1, and Day-2 Females

Reproductive stage of females	$\bar{x}$	p	q
Hydrated	4.6122	.2306	.7694
Day-1	3.1633	.1726	.8274
Day-2	2.7143	.1481	.8519

thereby reduce the variance of the estimate of spawning frequency. If their occurrence were random, the observed frequencies of day-1 and day-2 females should follow a positive binomial distribution. To test this assumption, we applied the Kolmogorov/Smirnov test (Siegel 1956). The frequencies of all three groups of females in different reproductive stages are listed in Table 3. Table 4 gives arithmetic means and the probability values *p* and *q* of the binomial distribution. The term *k* of the positive binomial distribution, the maximum number of individuals in a collection, was 20; in other words, 20 females per collection were included in the estimate of the frequency of hydrated, day-1, and day-2 females. The 5% significance level (D) for the Kolmogorov/Smirnov test is 0.1943, and the estimated maximum differences ($\hat{D}$) were 0.3628 (hydrated), 0.1656 (day-1), and 0.1859 (day-2). These results demonstrate that the frequencies of day-1 and day-2 females were not significantly different from the positive binomial distribution at the 5% level, whereas the hydrated females do not correspond to the positive binomial distribution. This becomes more obvious when the cumulative percentages of the observed and expected class frequencies of all three groups of females are plotted (Figure 4).

If the spawning frequencies of day-1 and day-2 females are to be combined, they must not be statistically different. To establish this we used a test of the difference between paired independent samples (Snedecor and Cochran 1967). The paired samples were the spawning frequency values of day-1 ($\hat{F}_1$) and day-2 ($\hat{F}_2$) females from each collection (Table 3). The null hypothesis was that the mean difference ($\bar{D}$) between $\hat{F}_1$ and $\hat{F}_2$ equals zero. $\bar{D}$ was 0.032. The t-test gave a value of 1.526 with n-1 = 48 degrees of freedom. This shows that the null hypothesis cannot be rejected at the 5% level of significance. Therefore, the two estimates can be combined, thus doubling the sample size.

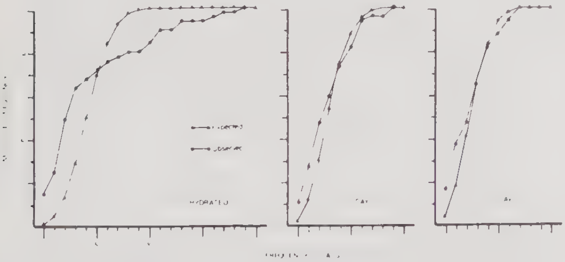

Figure 4. Cumulative frequencies of observed and expected (positive binomial distribution) class frequencies of females in different reproductive stages. The 49 collections of mature female anchovies are distributed into frequency classes according to the number of females they have in a particular reproductive stage (hydrated, day-1, or day-2); for example, in the left panel, frequency class 0 contains all collections having 0 hydrated females.

TABLE 5

Mean Percentage of Hydrated, Day-1, Day-2, and Day-1/Day-2 Females with Variance (V), Standard Deviation (SD), and Coefficient of Variation (CV)

Reproductive stage of females	Mean	V	SD	CV
Hydrated	.2306	1.2198×10^{-3}	.0349	.1515
Day-1	.1726	2.3248×10^{-4}	.0152	.0883
Day-2	.1481	1.7224×10^{-4}	.0131	.0886
Day-1 & day-2 (combined)	.1604	1.0175×10^{-4}	.0101	.0629

The spawning frequency of the day-1 females was 0.1726 with a variance of 2.3248×10^{-4}, a standard deviation of 0.0152, and a coefficient of variation of 0.0883 (Table 5). The spawning frequency of the day-2 females was 0.1481 with a variance of 1.7224×10^{-4}, a standard deviation of 0.0131, and a coefficient of variation of 0.0886. When these two data sets were combined, the estimate of spawning frequency was 0.1604 with a variance of 1.0175×10^{-4}, a standard deviation of 0.0101, and a coefficient of variation of 0.0629 (Table 5). By combining the data we have reduced the coefficient of variation by nearly a third. This would be important when the estimate of spawning frequency is used to calculate spawning biomass using the egg production method (Parker 1980; Stauffer and Picquelle 1980), because by reducing the coefficient of variation for spawning frequency one reduces the coefficient of variation for the biomass estimate (Santander et al., in press).

A spawning frequency of 16.04% (Table 5) means that in August/September 1981 the average mature Peruvian anchovy female spawned a new batch of eggs every 6.23 days. The high daily incidence of hydrated females (23.06%; Table 5) clearly indicates that hydrated females were oversampled. Comparing the coefficient of variation for the incidence of hydrated females with that of the day-1 and day-2 females indicates that the number of hydrated females per sample was much more variable than were the numbers of day-1 or day-2 females per sample.

Hydrated females also seem to be more vulnerable to the purse seine than other females. In order to test

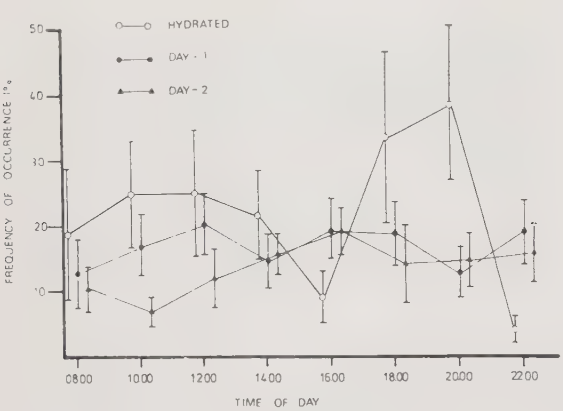

Figure 5. Change of percentage of frequency of occurrence of hydrated, day-1, and day-2 females in collections with time of day.

whether the three groups of females (hydrated, day-1, and day-2) show a diel change in their vulnerability to purse seining, the percentage of females in each group was calculated for 2-hour intervals and plotted at the midpoints of the 2-hour interval (Figure 5). The hydrated females had the highest percentage except for collections taken at about 1600 and at 2200 hours. The value at 2200 hours (4%) is low because most of the fish had completed spawning at that time. The very high values at 1800 hours (33%) and at 2000 hours (38%) indicate that hydrated females are particularly vulnerable at that time of day. At these hours, hydration of the ovaries has reached its maximum, and the ovaries are extremely heavy—in some cases up to 25% to 30% of the female's gonad-free body weight. The percentages of day-1 and day-2 females, on the other hand, remain relatively constant throughout the period, indicating that their vulnerability to capture does not change significantly with time of day.

Sex Ratio

The sex ratios (percentage of females on a weight basis) of all 49 collections showed large variations ranging from 12.62% to 90.50% females (Table 3). The average sex ratio was 56.43%, with a variance of 0.0007, a standard deviation of 0.0259, and a coefficient of variation of 0.0459. Similar variability in sex ratio of the northern anchovy has been reported by Klingbeil (1978), Hunter and Goldberg (1980), and Stauffer and Picquelle (1980). Klingbeil demonstrated that the greatest variability in the sex ratio occurs in the months of peak spawning. Hunter and Goldberg showed that sex ratio varied with spawning activity. We carried out the same analysis for the Peruvian anchovy.

We grouped all 49 collections into three classes based on their sex ratio. For each of these three classes we calculated the percentage of females in the following four spawning groups: (1) spawning on the night of capture (includes hydrated females and females with new postovulatory follicles), (2) day-1 females, (3) day-2 females, (4) females with no evidence of recent or imminent spawning (Table 6). In the male-dominated collections, which contained only 10% to 39% females, 54% of the females had spawned on the night of capture. On the other hand, in the female-dominated collections, where 70% to 99% of the fish were females, only 13% of the females had spawned on the night of capture. Correlation coefficients for sex ratio and (1) number of hydrated females, (2) number of day-1 females, and (3) number of day-2 females were −0.66, 0.35, and 0.34, respectively. Only the correlation coefficient of −0.66 for the hydrated females was significant at the 5% level. This shows that as the proportion of males in a collection increases, so does the proportion of hydrated females.

In addition, sex ratio also seemed to change with time of day. Most samples taken between 0700 and 1800 hours had 50% to 70% females, whereas after sunset (1800-2100 hours) the average ratio of females in the collections dropped below 50%. A similar pattern is described for the northern anchovy by Stauffer and Picquelle (1980). Average sex ratios (including all collections) computed for morning, afternoon, and night periods were 56.80%, 59.11%, and 54.25%, respectively (Table 7). These data show that the average sex ratio (56.43% females, $N = 49$) is probably biased by including those collections that have more than 30% hydrated females and were sampled at night. A more realistic sex ratio is computed by excluding all night collections sampled between 1800 and 2300

TABLE 6
Sex Ratio and Percentage of Females in Different Reproductive Stages

Sex ratio class (% females)	Number of collections	% Females				No. of females classified
		Spawning on day of capture	Day-1	Day-2	No evidence of spawning	
10-39	9	54	8	8	29	180
40-69	28	19	16	13	52	560
70-99	12	13	20	20	48	240

TABLE 7
Sex Ratios at Different Times of Day

Time of day	All collections		Excluding collections with >50% hydrated females		Excluding collections with >30% hydrated females	
	No. of collections	% of females	No. of collections	% of females	No. of collections	% of females
07.00-12.00	12	56.80	9	56.44	8	59.56
12.00-18.00	18	59.11	16	60.30	14	60.22
18.00-23.00	18	54.25	13	63.59	12	65.23

hours, the time of peak variability in sex ratio. From the remaining 30 collections we calculated a sex ratio of 57.90% with a variance of 0.0010, a standard deviation of 0.0311, and a coefficient of variation of 0.0536.

DISCUSSION

The spawning frequency of the Peruvian anchovy was found to be 16.04% in August-September 1981. This means that during the peak spawning period, Peruvian female anchovy spawn a new batch of eggs about once every six days. The spawning frequencies reported for the northern anchovy off California are somewhat lower: 14.5% in March-April 1980 (Stauffer and Picquelle 1980), 10.6% in February 1981 and 12.5% in April 1981 (Stauffer and Picquelle[2]), and 12.0% in January-March 1982 (Picquelle and Hewitt 1982). Hunter and Leong (1981) estimated that the northern anchovy spawns about 20 times per year; however, this has yet to be proven by an annual sampling program. These data on northern and Peruvian anchovy clearly contradict earlier assumptions that these two and other multiple-spawning pelagic species spawn only two or three times a year. Consequently, spawning biomass of such fishes has been considerably overestimated because of a severe underestimate of total fecundity (batch fecundity times spawning frequency).

Sex ratio is an important parameter for the application of the egg production method (Parker 1980), because of possible biases. The midwater trawl is reported to be a biased sampler with respect to sex ratio and hydrated females (Hunter and Goldberg 1980; Stauffer and Picquelle 1980). A higher-than-expected number of trawl samples had a high or a low number of females. In addition, hydrated females were twice as numerous as day-1 females. Stauffer and Picquelle[3] suggest that males and hydrated females segregate from other females at the hours of peak spawning at a depth where they are more vulnerable to the trawl.

The purse seine samples also appear to be biased in respect to sex ratio and numbers of hydrated females. In our study, oversampling of hydrated females occurred in the early morning hours, when the onset of hydration could be determined only by recording the migration of the oocyte nucleus to the pole. At this time, the oocytes have not increased perceptibly in size, and the ovary is only a small fraction of the total female weight. Three different explanations are possible for the oversampling of hydrated females in purse seines:

1. Hydration decreases the ability of female anchovies to avoid nets.
2. Females segregate vertically (by depth), and those with hydrated oocytes are more accessible to the purse seine than other females.
3. Females segregate horizontally (by area), and those with hydrated oocytes occur in different areas than those without hydrated oocytes.

In any case, using the incidence of hydrated females to estimate spawning frequency for anchovy (suggested by Hunter and Macewicz 1980) seems an inaccurate procedure, even if day samples of anchovies can be obtained.

The sex ratio in the 49 collections ranges from 12.62% to 90.50% females, with an average of 56.43% (Table 3). Night purse seine collections with a high percentage of hydrated females (with respect to the female fraction) also contain a high percentage of males. Hydrated females are oversampled both day and night, but the co-occurrence of high percentages of hydrated females and of males is recorded only at night. It might be hypothesized that the high male ratio in these night collections is because hydrated females, which are about to spawn, are attractive to and surrounded by a high number of males (Hunter and Goldberg 1980). If the hypothesis is correct that hydrated females are caught more often (than expected) because their vulnerability to the net increases, then only the hydrated females should be oversampled and not the males as well. Thus it seems more likely that the hydrated females segregate, either by depth or by area, from the "normal" school, taking a high percentage of males with them and forming "spawning schools" dominated by males.

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[2] Stauffer, G.D., and S.J. Picquelle. The 1981 egg production estimates of anchovy spawning biomass. Unpublished manuscript, 29 p. NMFS, Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038.

[3] Ibid.

The average sex ratio is biased because the night collections contain a high percentage of hydrated females. When these collections are omitted, the average sex ratio rises to 57.90%. If the true sex ratio of the population is 50% female, the purse seine clearly oversamples females, whereas the trawl seems to undersample them slightly (Stauffer and Picquelle 1980; Picquelle and Hewitt 1982). Klingbeil (1978) reported similar findings when he compared the sex ratios of anchovy obtained from commercial purse seiners (females:males = 1.60:1) and from research trawlers (females:males = 1.09:1). He suggested that the male-dominated schools may not form the large dense aggregations required for effective purse seining. This might also explain the difference in sex ratios between the northern and the Peruvian anchovy collections. The large Peruvian purse seiner (270 tons) may have shot the seine when the echo sounder indicated a relatively large, dense, female-dominated school, whereas each California trawl sample collected fish from a much larger area. Thus the trawl samples included more male-dominated spawning schools, which presumably are less dense and extend over a much larger area. Therefore, if spawning schools are segregated horizontally from normal schools, the trawl may be a more suitable tool for determining the sex ratio of anchovies than a purse seine.

Interpreting the different effects of trawling and seining on sampling of hydrated females is difficult. They were oversampled by the Peruvian purse seiner in 1981 and by the California trawler in 1980 and 1981 (Stauffer and Picquelle 1980; Stauffer and Picquelle[4]). However, hydrated females were not oversampled by the California trawler in 1982, possibly because the trawl may have fished a shallower depth (Picquelle and Hewitt 1982). The oversampling of hydrated females might be solved by a comparative study between a purse seiner and a larger midwater trawler, which allows fishing in depths not reached by a purse seine.

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[4] See footnote 2 on page 51

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THREE NEW SPECIES OF *LENSIA*, AND DESCRIPTION OF THE EUDOXIA STAGES OF *LENSIA RETICULATA* AND *LENSIA LELOUVETEAU* (CALYCOPHORAE: SIPHONOPHORAE)

Angeles Alvariño and Joan Marie Wojtan

Abstract.—Three new species of *Lensia* are described and illustrated: *Lensia eugenioi*, *L. eltanin*, and *L. landrumae*, their diagnostic characteristics are discussed and compared with those of other closely related species of *Lensia*. The previously unknown eudoxid stages of *Lensia reticulata* Totton, 1954, and *L. lelouveteau* Totton, 1941, are also described and illustrated. The specimens were observed in plankton collections obtained during the U.S. Antarctic Research Program.

Lensia Totton

Diagnosis.—The genus *Lensia* Totton, 1932 includes diphyid Calycophorae in which the anterior nectophores of the polygastric stage are pentagonal in cross section, but may exhibit 3, 5, 7, 15, or more longitudinal ridges, with or without crests or wings. The somatocyst is usually short. The hydroecium is shallow, and is closed by short, divided mouth plates. The radial canals have no commissures. The nectosac reaches to near the top of the nectophore.

The posterior nectophore is known for only a few species. It is truncate at the top, has a rounded mouth plate, and no conspicuous teeth. The lateral radial canals are not looped, but run in an open S course.

Only a few eudoxid stages of *Lensia* have been described.

There are 24 previously described species of the genus *Lensia*, and with the three new ones there will be 27. The known species of *Lensia* are: *Lensia achilles* Totton, 1941; *L. ajax* Totton, 1941; *L. bary* Totton, 1965; *L. campanella* (Moser, 1925); *L. challengeri* Totton, 1954; *L. conoidea* (Kefferstein and Ehlers, 1860); *L. cordata* Totton, 1965; *L. cossack* Totton; 1941; *L. exeter* Totton, 1941; *L. fowleri* (Bigelow, 1911); *L. grimaldii* Leloup, 1933; *L. hardy* Totton, 1941; *L. havock* Totton, 1941; *L. hostile* Totton, 1941; *L. hotspur* Totton, 1941; *L. hunter* Totton, 1941; *L. leloupi* Totton, 1954; *L. lelouveteau* Totton, 1941; *L. meteori* Leloup, 1934; *L. multicristata* (Moser, 1925); *L. reticulata* Totton, 1954; *L. subtilis* (Chun, 1886); *L. subtiloides* (Lens and van Riemsdijk, 1908); *L. tottoni* Daniel and Daniel, 1963. (See Alvariño 1971 for distributions.)

Material.—Collections in which the new species here described were found, were obtained during the *Eltanin* cruises of the U.S. Antarctic Research Program, using plankton nets: BPS (bathypelagic plankton sampler), MPS (multiple plankton sampler), vertical (V) or oblique (OBL) plankton tows (see Tables 1–5).

Lensia eugenioi, new species
Fig. 1

Material.—(See Table 1.) Holotype: 1 superior nectophore and 1 inferior nectophore, *Eltanin* cruise 26, sta. 1785, USNM 61058: paratype, 2 superior nectophores and 2 inferior nectophores, *Eltanin* cruise 26, sta. 1803, USNM 61059.

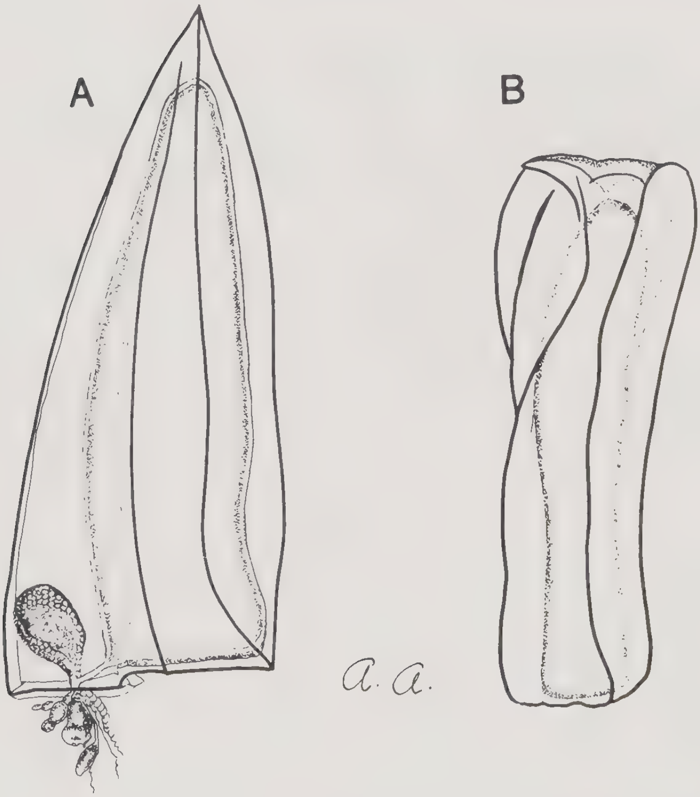

Fig. 1. *Lensia eugenioi*: A, Lateral view of superior nectophore (5 mm long); B, Ventrolateral view of inferior nectophore (4.5 mm long).

Etymology.—Named for Captain Eugenio Leira, the husband of the senior author.

Description.—The length of the superior nectophore is approximately 3 times its width. The nectosac reaches close to the top of the nectophore. There are 5 complete ridges with crests extending from the opening of the nectosac (the ostium), to the top of the nectophore: 2 ventral and 2 lateral (one at each side, corresponding to the dorsoventral), and one dorsal. In addition, 2 other lateral ridges, the ventrolateral, extend from the ostium to near the top of the nectophore, up to the level of the top of the nectosac, but do not reach the top of the bell. These incomplete ventrolateral ridges are similar to those in *L. multicristata,* although in the latter the ridges do not reach either the apex or the marginal base of the nectophore. In *L. eugenioi* they reach to the basical margin of the ostium, but not to the apex. The dorsolateral ridges of *L. eugenioi* bend sharply at the low part near the ostium region, reaching the dorsal edge of the nectophore at this point joining the dorsal ridge.

The hydroecium is very shallow, tapering to the ventral side. Two very small flaps close the opening of the hydroecium at the side of the ostium.

Table 1.—Distribution of *Lensia eugenioi* in the Antarctic-Subantarctic region.

Cruise	Station	Gear/tow	Location	Depth of haul	Date	Local time
26	1785	MPS	39°47′S, 160°30′E	250–100 m	5 Dec 1966	1112–1117
	1790	V	41°58′S, 160°06′E	200–0 m	7 Dec 1966	1351–1412
	1794	BPS	41°58′S, 160°06′E	1000–500 m	7 Dec 1966	1425–1449
	1803	BPS	47°37′S, 161°49′E	1000–500 m	13 Dec 1966	1052–1112

The somatocyst is thick, short, and pear-shaped.

The radial canals extend along the dorsal and ventral edges of the nectosac to join the circular canal, and other branches extend along each of the sides of the nectosac, from the pedicular canal to near the top of the nectosac. These branches probably bend, to run down to reach the circular canal (Fig. 1A).

The inferior nectophore (Fig. 1B) is prismatic, with 5 longitudinal ridges. The region of the hydroecium is closed at the upper part by the flaps extending from the ridges, which cover each other to form the hydroecial tunnel. There are no teeth or prolongations at the ostium region. The lateral radial canals follow a sigmoid course.

Eudoxid phase: Unknown.

Lensia eltanin, new species

Fig. 2

Material.—(See Table 2.) Holotype: 1 superior nectophore, 1 inferior nectophore, *Eltanin* cruise 11, sta. 263, USNM 61060; paratype: 1 superior nectophore and 2 inferior nectophores, *Eltanin* cruise 11, sta. 263 and 308, USNM 61061.

Etymology.—Named for the USNS *Eltanin,* which for many years has surveyed the Antarctic Ocean and adjacent oceanic regions; the present collections were obtained during this vessel's cruises in Antarctic and Subantarctic waters.

Description.—This species also belongs to the group of the previously described species, based on the characteristics of the lateral ridges.

The superior nectophore (Fig. 2A) reaches a length of about 6 to 7 mm, with a maximum width of 3 mm at the ostium. It has 5 complete ridges extending from the tip of the nectophore to the ostium. All the ridges have a narrow crest. The dorsal ridge forms a small tooth at the margin of the ostium, but does not form a marked tooth-like projection, due in part to the crest of the ridge covering that area. The lateral ridges bend sharply to the ventral side and then to the dorsal side at the lowest part of the nectophore, and reach the margin of the nectophore at about midlength of the ostium opening, between the hydroecium and the dorsal ridge.

The nectosac reaches close to the top of the nectophore.

The hydroecium is deeper than in *Lensia conoidea.* The hydroecial cavity is large, reaching to a point slightly higher than the level of the ostium, and wide, as in *L. conoidea.* The hydroecium is slightly shallower than a hemisphere, and is closed at the dorsal side, adjacent to the ostium, by 2 flaps. There is a wide distance from the ventral edge of the nectosac to the ventral edge of the nectophore, as is seen in *L. conoidea.*

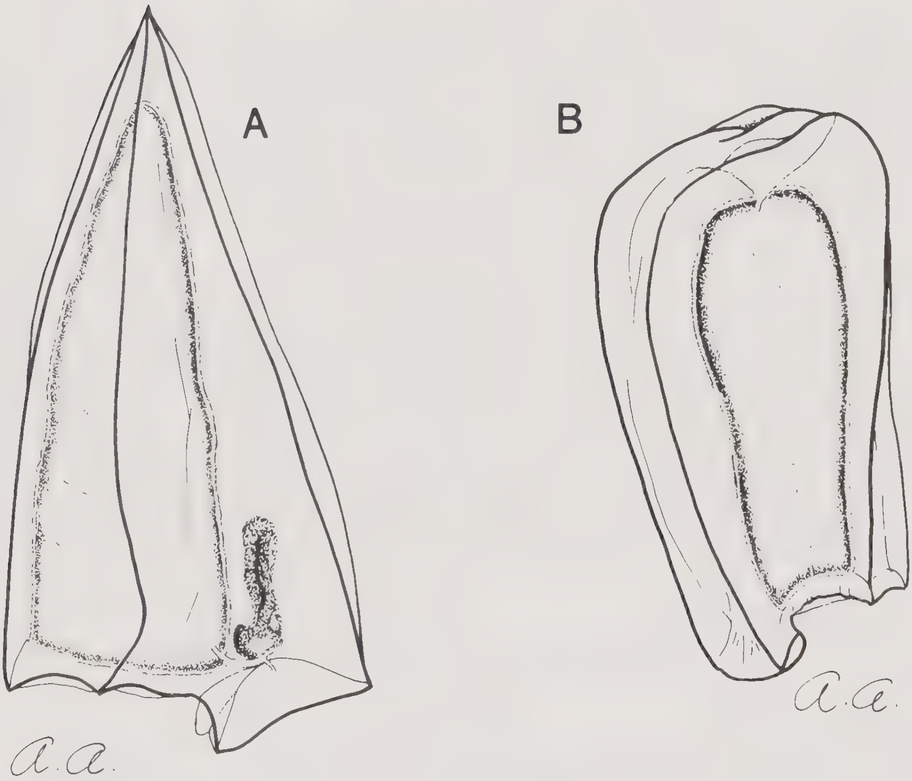

Fig. 2. *Lensia eltanin*: A, Lateral view of superior nectophore (6–7 mm long); B, Lateral view of inferior nectophore (4.7 mm long).

The somatocyst is of medium length, reaching about ⅕ of the total length of the nectophore. The somatocyst is wider at the base, and the branch that goes up is about ½ the width of the basal part of the somatocyst.

The posterior nectophore (Fig. 2B) presents 5 ridges: 2 ventral, 1 dorsal, and 2 lateral. Those forming the hydroecium are wide, wing-like; they bend, closing that area, and extend down to the level of the ostium, where they are connected

Table 2.—Distribution of *Lensia eltanin* in the Antarctic-Subantarctic region.

Cruise	Station	Gear/tow	Location	Depth of haul	Date	Local time
11	257	MPS	60°56′S, 114°43′W	500–250 m	5 Jan 1964	1451–1532
	263	BPS	61°58′S, 115°11′W	1000–500 m	7 Jan 1964	0835–0949
	308	MPS	70°07′S, 102°55′W	500–250 m	20 Jan 1964	2019–2044
	309	BPS	70°07′S, 102°52′W	1000–500 m	20 Jan 1964	2202–2308
	310	OBL	70°25′S, 99°21′W	550–0 m	22 Jan 1964	0332–0435
15	864	BPS	54°00′S, 145°17′W	1000–500 m	18 Nov 1964	~1000
16	900	MPS	51°09′S, 162°00′E	500–250 m	8 Feb 1965	1525–1535

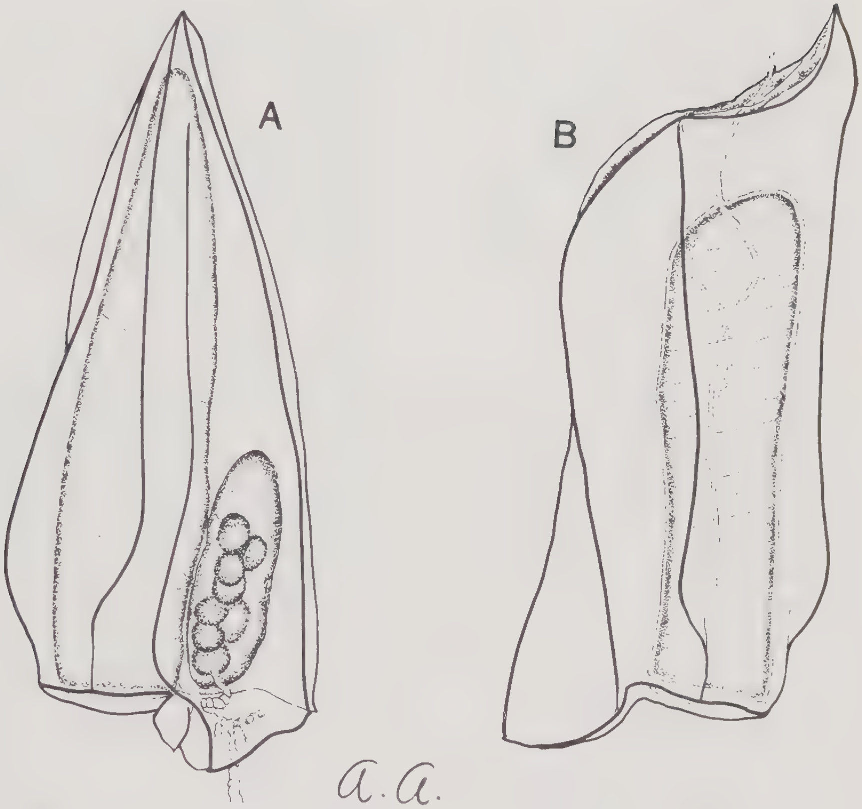

Fig. 3. *Lensia landrumae*: A, Lateral view of superior nectophore (6 mm long); B, Lateral view of inferior nectophore (4.8 mm long).

by the basal wing which is slightly lower than the ostium level. The posterior and lateral ridges are also crested, and end in small, tooth-like formations.

The radial canals follow the typical sigmoid pattern for the genus, and join the circular canal.

The apex of the posterior nectophore is roundish, with the dorsal side higher than the ventral, fitting perfectly in the hydroecium of the first nectophore.

Eudoxid phase: Unknown.

Lensia landrumae, new species
Fig. 3

Material.—(See Table 3.) Holotype: 1 superior nectophore and 1 inferior nectophore, *Eltanin* cruise 21, sta. 1403, USNM 61062; paratype: 2 superior nectophores and 2 inferior nectophores, *Eltanin* cruise 16, sta. 925, and cruise 26, sta. 1794, USNM 61063.

Etymology.—Named for Elizabeth Landrum, in recognition of her dedication throughout the years to advancing plankton studies, and her encouragement and valuable assistance to this research.

Table 3.—Distribution of *Lensia landrumae* in the Antarctic-Subantarctic region.

Cruise	Station	Gear/tow	Location	Depth of haul	Date	Local time
10	192	V	56°57′S, 74°58′W	992–0 m	11 Nov 1963	1651–1739
16	884	BPS	44°21′S, 162°00′E	1000–500 m	4 Feb 1965	1350–1406
	895	MPS	49°17′S, 162°00′E	500–250 m	7 Feb 1965	1110–1124
	925	MPS	52°26′S, 166°42′E	250–100 m	18 Feb 1965	1552–1558
21	1403	MPS	54°06′S, 119°54′W	500–250 m	20 Dec 1965	0035–0045
26	1794	BPS	41°58′S, 160°06′E	1000–500 m	7 Dec 1966	1425–1449
	1803	BPS	47°37′S, 161°49′E	1000–500 m	13 Dec 1966	1052–1112

Description.—The superior nectophore (Fig. 3A) is about 6 mm high and 2.5 mm in width. There are 5 complete ridges extending from tip of the nectophore to the region of the ostium: 2 ventral, 1 dorsal, and 2 dorsolateral. Another pair of ridges, the ventrolateral, extend from the region of the pedicel (where the margin of the nectosac is adjacent to the hydroecium), up to near the top of the nectophore. The ventrolateral ridges do not reach the top of the nectophore. The dorsal ridge and the dorsolateral ridges have crests, which are widest at the low part of the ridge, but the crests disappear from this region to the level of the ostium. This low portion of the ridge has no crest; the portion with no crest is about ⅛ of the length of the nectophore. The ventrolateral ridges present a round crest at the lowest part, that is, at the ostium region, diminishing in width as they reach the upper part of the nectophore.

The somatocyst is large, massive and globular-oval in shape, in contact with ventral wall of the nectosac.

The hydroecium is deep, but reaches to the level of the ostium, and is closed by two flaps on the dorsal side.

The region of the somatocyst between the nectosac and the ventral ridges is filled with mesoglea, as is seen in *L. conoidea.*

The posterior nectophore (Fig. 3B) is prismatic, with 5 ridges having the same characteristic features as the superior nectophore. The upper part of the nectophore extends in a triangular peak on the dorsal side. The crests of the dorsal and lateral ridges widen near the ostial region, but the lowest part has no crest, showing a pattern similar to that of the superior nectophore. The ventral ridges are wing-like, closing the hydroecium, which resembles a tunnel.

The anterior and posterior radial canals are straight, running from the pedicel at the top of the nectophore, to the ring canal. The lateral radial canals bend in a step-like shape at the upper part of the nectosac, and run down straight to the ring canal.

Because the characteristics of the ridges and crests of this inferior nectophore are similar to those in the superior nectophore of *L. landrumae* n. sp., it is assumed that these inferior nectophores correspond to that species.

The eudoxid phase is unknown.

Discussion.—The species closely related to *L. eugenioi* and *L. eltanin* are *L. achilles, L. bary,* and *L. cordata.* In *L. achilles* the somatocyst is a somewhat elongate spindle-shaped club. The lateral ridges are just at midwidth of the lateral sides, bending ventrally and then dorsally to reach to the dorsal ⅓ of the ostium

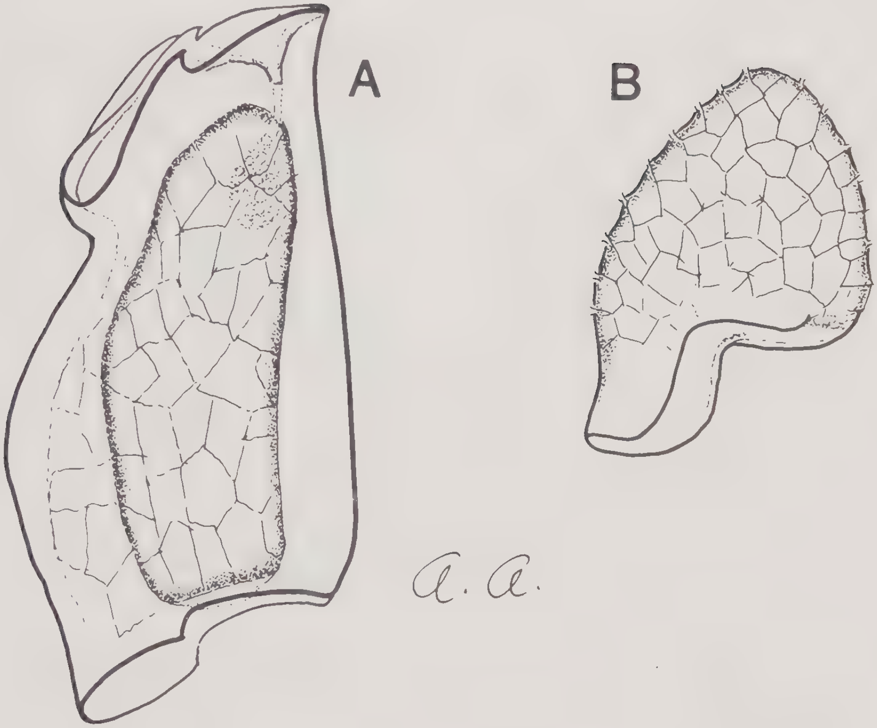

Fig. 4. *Lensia reticulata*: A, Lateral view of gonophore (2.5 mm long); B, Bract (1.6 mm high).

margin. The hydroecial cavity is deep, exhibiting the same depth from the dorsal to the ventral side of the cavity. The top of the hydroecium is level with the ostium; on the dorsal of the proximal part of the ostium, the top of the hydroecium is slightly higher than the ventral side, or distal part of the ostium.

In *Lensia bary* the somatocyst exhibits a large spindle or inverted club shape. There is an elongate globular oval with a small ampullar projection at the top. Lateral ridges are slightly bent at the ostium region (less sharply bent than in *L. achilles*), reaching the middle of the ostium region. The hydroecium is as deep as in *L. achilles,* but shallow toward the ventral side (the part far from the ostium). The top of the hydroecium is level with the ostium.

Lensia cordata has lateral ridges bending sharply to the dorsal side, reaching one-fourth of the dorsal ostium region. The somatocyst is heart-shaped, on top of a short peduncle. The heart-shaped part begins level with or slightly higher than the ostium. The hydroecium is shallower than in *L. achilles* and *L. bary,* ending just at the level of the ventral ridges.

Lensia cordata has longitudinal ridges with crests, while crests are not present in *L. bary* and or *L. achilles.*

One of the main differential characteristics of the above-mentioned group of species of *Lensia* is the position of the end of the lateral ridges at the ostium region. In *L. achilles* that point is at one-third of the dorsal side, in *L. bary* at

Table 4.—Distribution of eudoxids of *Lensia reticulata* in the Antarctic-Subantarctic region.

Cruise	Station	Gear/tow	Location	Depth of haul	Date	Local time
10	165	V	65°00′S, 74°58′W	2035–0 m	1 Nov 1963	0350–0455
11	249	BPS	58°57′S, 114°45′W	1000–500 m	3 Jan 1964	0132–0233
	253	MPS	59°56′S, 114°56′W	480–250 m	4 Jan 1964	0220–0304
	254	BPS	59°55′S, 114°56′W	1000–250 m	4 Jan 1964	0350–0502
	257	MPS	60°56′S, 114°42′W	500–250 m	5 Jan 1964	1451–1532
	262	MPS	61°56′S, 115°12′W	500–250 m	7 Jan 1964	0714–0754
	268	MPS	62°57′S, 115°16′W	500–250 m	8 Jan 1964	0738–0821
	292	BPS	68°20′S, 114°47′W	unknown	15 Jan 1964	2237–0000
	303	BPS	70°09′S, 106°40′W	1000–500 m	19 Jan 1964	1946–2103
	308	MPS	70°08′S, 102°55′W	500–250 m	20 Jan 1964	2019–2044
	320	BPS	67°58′S, 90°54′W	1000–500 m	26 Jan 1964	0822–0929
	326	BPS	65°55′S, 89°06′W	1000–500 m	28 Jan 1964	0625–0730
15	881	MPS	57°00′S, 150°08′W	500–250 m	21 Nov 1964	2112–2131
16	895	MPS	49°17′S, 162°00′E	500–250 m	7 Feb 1965	1110–1124

about the middle of the ostial opening, in *L. cordata* at one-fourth of the dorsal side, in *L. eugenioi* at the dorsal side, and in *L. eltanin* at about midlength of the ostium.

The hydroecium is different in shape and size for all five closely related species, and the shape and size of the somatocyst is also different in each of the species.

Lensia eugenioi is the only one in the group with five complete ridges and two additional ridges (ventrolateral), which go from the ostium to near the top of the nectophore, not reaching the apex.

Lensia landrumae is different from any of the previously described species of the genus *Lensia* in the shape of ridges and crests, hydroecium, and somatocyst.

Lensia reticulata Totton, 1954
Fig. 4

Diagnosis.—The nectophores are multicristate, with cross-connecting ridges forming an irregular meshwork.

The superior nectophore of the polygastric phase has been described (Totton 1954). The eudoxid phase has not been previously described.

Material.—Specimens of the eudoxid phase of *Lensia reticulata* were observed in collections from *Eltanin* cruises listed in Table 4. Voucher material of eudoxid phase, 1 bract and 1 gonophore, cruise 11, sta. 308, USNM 61068; 1 bract, 2 gonophores, cruise 11, sta. 326, and cruise 15, sta. 881, USNM 61069.

Description.—The gonophore (Fig. 4A) is an oval, with a roundish area at the top where the bract is attached. The walls of the gonophore are thin, and have a reticular pattern similar to that of the polygastric nectophore.

The bract (Fig. 4B) is like a cap, formed by two parts; the top or hemispherical cover is of thick mesoglea, covered by a thick network of ridges, like a honeycomb; the visor part is wide. The visor part attaches to the groove at the top of the gonophore.

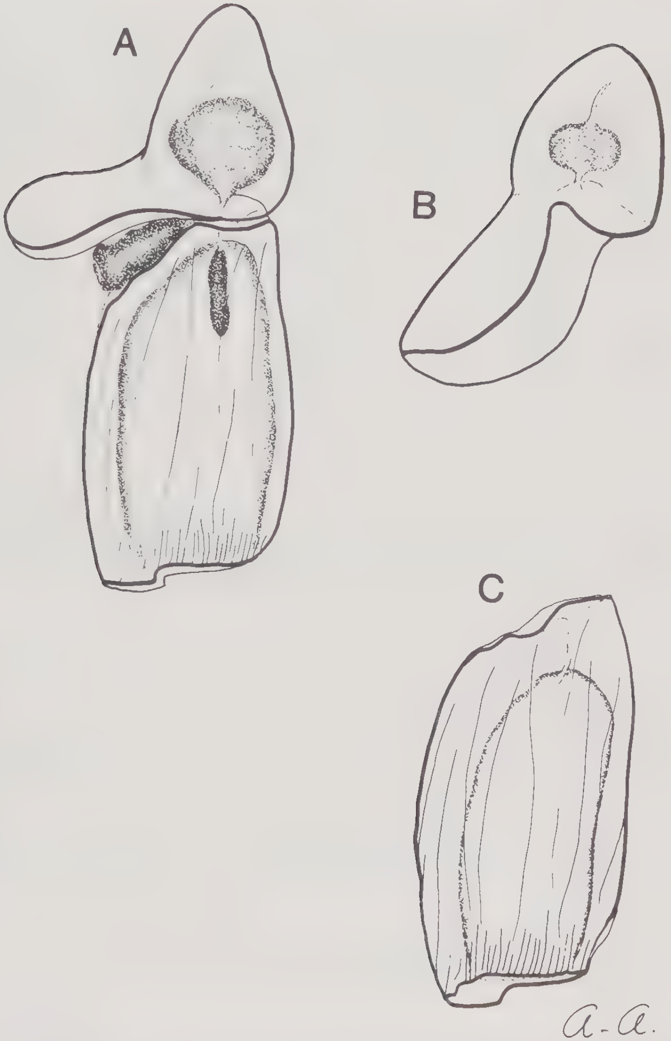

Fig. 5. *Lensia lelouveteau*: A, Complete eudoxid (5 mm long); B, Bract (2.5 mm long); C, Gonophore (3 mm long).

Lensia lelouveteau Totton, 1941
Fig. 5

Diagnosis.—The eudoxid phase of *Lensia lelouveteau* has not been previously described. The specimens found could belong to this species, based on the multicristate pattern of the ridges and the particular feature of a band of ridges at the inferior part of the gonophore, all of which makes this gonophore very similar to the description and characteristics of the superior nectophore of *L. lelouveteau* Totton, 1941.

Table 5.—Distribution of the eudoxid phase of *Lensia lelouveteau* in the Antarctic-Subantarctic region.

Cruise	Station	Gear/tow	Location	Depth of haul	Date	Local time
10	196	V	65°21′S, 75°02′W	2045–0 m	13 Nov 1963	0702–0838
11	253	MPS	59°57′S, 114°57′W	480–250 m	4 Jan 1964	0220–0304
	257	MPS	60°56′S, 114°43′W	500–250 m	5 Jan 1964	1451–1532
	268	MPS	62°58′S, 115°17′W	500–250 m	8 Jan 1964	0738–0821
	308	MPS	70°07′S, 102°55′W	500–250 m	20 Jan 1964	2019–2044
	326	BPS	65°55′S, 89°08′W	1000–500 m	28 Jan 1964	0625–0730
16	900	MPS	51°09′S, 162°01′E	500–250 m	8 Feb 1965	1526–1535
	926	MPS	52°26′S, 166°42′E	500–250 m	18 Feb 1965	1544–1552
21	1403	MPS	54°03′S, 119°54′W	500–250 m	20 Dec 1965	0035–0045
26	1794	BPS	41°58′S, 160°06′E	1000–500 m	7 Dec 1966	1425–1449
	1803	BPS	47°37′S, 161°49′E	1000–500 m	13 Dec 1966	1052–1112

Material.—Complete eudoxid specimens (bract and gonophore attached), and bracts and gonophores free, disentangled, have been observed in plankton collections obtained by *Eltanin* cruises listed in Table 5. Voucher material: 1 complete eudoxid, cruise 16, sta. 900, USNM 61070; 4 eudoxids, 3 bracts, 5 gonophores, cruise 16, sta. 926, and cruise 11, sta. 268, USNM 61071.

Description.—The bract (Fig. 5A, B) has a conical top of thick mesoglea, with wide, round, wing-like shield at the ventral side. At the union of the conical body and the laminar wing or bracteal margin, the body is contracted into a neck-like shape. This laminar wing may cover more than half the height of the gonophore. The phylocyst is globular in shape. The hydroecial cavity is conical and shallow.

The gonophore (Fig. 5C) is cylindrical, with a short top platform which adjusts to the cavity of the bract, extending at the ventral side into a flattened triangular shape, where other parts of the eudoxid are located. The walls of the gonophore are covered by ridges similar to those found in the nectophore of the polygastric form of *Lensia lelouveteau.*

It appears that there is no asexual swimming bell; gonads were observed inside the gonophore, which acts as a swimming bell.

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8407

Mortality Estimation: Biased Results from Unbiased Ages

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Barlow, J. 1984. Mortality estimation: biased results from unbiased ages. Can. J. Fish. Aquat. Sci. 41: 1843–1847.

Estimates of mortality rates from age distributions are biased by imprecision in age estimation, even if age estimates are unbiased. I have derived a method for predicting the magnitude of this bias from information on the precision of age determination. Monte Carlo simulations show that bias can be accurately predicted. The commonly used Chapman–Robson mortality estimator is shown to be robust to imprecision in age determination if all age-classes are included. Errors are likely, however, if one or more age-classes are excluded or if other mortality estimators are used. Biases can be corrected if the distribution of age-estimation errors is known.

L'estimation des taux de mortalité d'après les distributions des âges est biaisée en raison de l'imprécision de la détermination de l'âge, même si les estimations des âges ne sont pas biaisées. Nous avons mis au point une méthode par laquelle on peut connaître l'importance de ce biais d'après des renseignements sur la précision de la détermination de l'âge. Les simulations de Monte Carlo révèlent qu'il est possible de déterminer le biais avec exactitude. Nous avons constaté que l'estimation de Chapman–Robson, qui est couramment employée pour déterminer la mortalité, peut absorber l'imprécision de la détermination de l'âge lorsqu'on emploie toutes les classes d'âge. Toutefois, il est probable qu'il y ait des erreurs si l'on exclut une ou plusieurs classes d'âge ou si l'on emploie d'autres estimateurs pour déterminer la mortalité. Il est possible de corriger le biais si l'on connaît la distribution des erreurs des estimations de l'âge.

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Age–frequency distributions have frequently been used to estimate mortality rates via an application of stable population theory. Many methods have been proposed for extracting this mortality information from age distributions (Deevey 1947; Chapman and Robson 1960; Caughley 1966; Barlow 1982). All of these methods have assumed that ages could be determined without error. In fact, error in age estimation is a very real problem (Beamish and Fournier 1981; Chang 1982). Clearly, mortality rates could be biased if age estimation is biased. Here I address a slightly different question: can biased mortality estimates result from imprecise, but unbiased ages?

The assumptions required for estimating mortality rate (or its complement, survival rate) from age frequencies are stringent. Stated briefly, a population must be in stable age distribution and its growth rate must be known. These assumptions are treated in detail elsewhere (Caughley 1966; Barlow 1982). Despite stringent assumptions, use of these methods is common in fishery, marine mammal, and other wildlife research. The assumption of accurate age determinations has always been implicit, though usually unspoken.

Given a population with a zero growth rate, a stable age distribution, and a constant mortality rate with age, Chapman and Robson (1960) have derived a minimum variance, unbiased estimator of that population's survival rate based solely on sampled age frequencies. Because the Chapman–Robson (C–R) method is unbiased in cases where aging is deterministic, this method was chosen to examine potential biases when errors occur in age determination. Standard errors of the predicted survival rates can also be estimated from the C–R method.

The C–R survival rate estimator can be expressed in vector notation as

$$(1)\quad \hat{s} = \boldsymbol{n}\cdot\boldsymbol{v}' \Big/ \left(\sum_{i=1}^{\infty} n_i + \boldsymbol{n}\cdot\boldsymbol{v}' - 1 \right)$$

where $\boldsymbol{n}$ is the vector of observed frequencies by age-class and v is a vector defined such that $v_i = i - 1$. This survival rate estimator can be reformulated in terms of two parameters: sample size and a scaled mean age (Chapman and Robson 1960, Eq. 4). It is trivial to show that an unbiased error in estimating ages will not affect the expected value of the scaled mean age. Imprecision in estimating ages will, therefore, not affect the expected value of C–R survival rate if all age-classes are included. Frequently the first several age-classes are excluded because their abundance cannot be estimated without bias (e.g. Barlow 1982, Chap. 1). The exclusion of the first age-classes can introduce a bias in the estimation of survival rates when age estimation is subject to errors. In this paper, I derive an expression that predicts the magnitude of this bias and use Monte Carlo simulations to verify the ability of this expression to predict bias accurately.

I only consider the special case for which age estimation is unbiased. In fact, there are few situations where the probability of counting too many annual layers would equal the probability of counting too few. It will be assumed that these types of errors can be corrected with calibration studies.

Methods

To remain consistent with the terminology of Chapman and Robson (1960) and common usage, ages and errors in ages are represented as discrete integers (days, years, etc.). The distribution of aging errors is seldom uniform over all ages. Most commonly, young animals can be aged with greater precision than older animals. The probability distribution of age estimates for a given age-class can be given as columns of a transition probability matrix (e.g. Table 1). The (i, j)th element of such a matrix, $\boldsymbol{P}$, would represent the probability that an individual in age-class j would be interpreted as belonging to age-class i. The product of the transition matrix times the true age distribution of a sample, $\boldsymbol{n}$, would thus give the age distribution that might be expected to be observed given $\boldsymbol{n}$, $\boldsymbol{m}$:

$$(2)\quad \boldsymbol{P}\cdot\boldsymbol{n} = \boldsymbol{m}.$$

The observed age distribution would be expected to differ from the true age distribution unless (trivially) $\boldsymbol{P}$ is the identity matrix, or (miraculously) $\boldsymbol{n}$ is an eigenvector of $\boldsymbol{P}$ with a unit eigenvalue.

When errors in aging are considered, the expected C–R survival rate could be estimated by substituting $\boldsymbol{m}$ for $\boldsymbol{n}$ in Equation 1:

$$(3)\quad \hat{s} = \frac{\boldsymbol{m}\cdot\boldsymbol{v}'}{\sum_{i=k}^{\infty} m_i + \boldsymbol{m}\cdot\boldsymbol{v}' - 1}$$

where k is the first age-class included in the estimation and v is defined such that $v_i = 0$ if $i \leqslant k$, and $v_i = i - k$ if $i > k$.

In this study, the expected value of $\hat{s}$ was calculated for a range of values of the actual survivorship ($s = 0.25$–0.75) and the first age-class to be included ($k = 1$–10). The expected age distribution of a sample was estimated as the geometric series corresponding to the true survivorship. The distribution of aging errors was determined by the probability transition matrix (Table 1). For all ages, the aging errors were symmetric about the true age; hence, the expected age of any individual would equal its true age. Biases due to aging errors were estimated as the difference between the survival rate calculated using Equations 2 and 3 and the true survival rate.

TABLE 1. Probability distributions of aging errors by age-class. Elements indicate the probability that an individual with a given true age will be assigned to the indicated categories of estimated age. Note that errors are symmetrically distributed about the principle diagonal within columns. Note also that aging precision is assumed constant for individuals older than 6.

Estimated age	True age 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	·	·	·
1	1.0	0.1																
2		0.8	0.2	0.1	0.1	0.1												
3		0.1	0.6	0.2	0.1	0.1	0.1											
4			0.2	0.4	0.2	0.1	0.1	0.1										
5				0.2	0.2	0.1	0.1	0.1	0.1									
6				0.1	0.2	0.2	0.1	0.1	0.1	0.1								
7					0.1	0.1	0.2	0.1	0.1	0.1	0.1							
8					0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1						
9						0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1					
10						0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1				
11							0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1			
12								0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	·	·	·
13									0.1	0.1	0.1	0.1	0.2	0.1	0.1			
14										0.1	0.1	0.1	0.1	0.2	0.1			
15											0.1	0.1	0.1	0.1	0.2			
·												·				·		
·												·					·	
·												·						·

Monte Carlo simulations were used to test the ability of the described procedures to estimate bias resulting from errors in age determinations. Age distributions were generated by randomly drawing discrete samples (with replacement) from a population with a geometric series distribution. This is analogous to a population with constant recruitment and with a survival rate that does not vary with age. In order to mimic error in age determination, a random integer was added to or subtracted from each age selected from the population. Again the distribution of errors was taken from Table 1.

For purposes of illustration, mean values of the C–R estimate were calculated from simulations using three different survival rates (0.3, 0.5, and 0.7) and three different starting ages (1, 2, and 3). These fall within the range of values used in the deterministic approach. The simulation was run with 1000 age distributions (with errors) for each of these nine permutations. Sample sizes for "aged" individuals of all age-classes were set so that the nominal sample for survival rate estimation was 200. Survival rates were only estimated for those individuals whose "apparent" age was greater than or equal to a given starting age (1, 2, or 3); hence, sample size varied slightly about this nominal value due to stochastic effects. Means and standard deviations of survival rates were calculated for each set of 1000 age distributions.

Results

The expected survival rate estimates from the C–R method are shown in Fig. 1 for a range of true survival rates and number of excluded age-classes. As predicted, the method is unbiased if all age-classes are included. If the initial age-class(es) are excluded, an appreciable bias can result. For the given error matrix, the magnitude of this bias is greater when survival rates are low and smaller when survival rates are high. When the first included age-class is 10 or greater, the bias disappears completely.

The results of the Monte Carlo simulation confirm these results. The average survival rates estimated using the C–R method are given in Table 2 for each of the nine combinations of true survival rates and starting ages. Each represents the average estimate from 1000 randomly selected age distributions with simulated error in age determination. Also tabulated are the survival rates predicted using Equations 2 and 3 and the expected (geometric series) age distributions. The magnitude of the bias observed in the simulations was in good agreement with the bias predicted from Equation 3. Observed standard errors in the survival rate estimates were only trivially different from those predicted by the C–R formulations (J. Barlow, unpubl. data).

Discussion

Age distributions typically resemble a declining exponential function. Errors in aging will usually change the shape of such a

TABLE 2. Results of Monte Carlo simulations of survival rate estimation with errors in age determinations. Mean survival rate estimates are averages of 1000 C–R estimates from randomly selected and transformed age distributions. Predicted survival rate estimates are from Equations 2 and 3, using a geometric series age distribution (corresponding to the actual survival rate) for n.

	First age-class included 1	2	3
s	0.3	0.3	0.3
Mean $\hat{s}$	0.2993	0.3492	0.3589
Predicted $\hat{s}$	0.3000	0.3490	0.3597
s	0.5	0.5	0.5
Mean $\hat{s}$	0.4995	0.5254	0.5452
Predicted $\hat{s}$	0.5000	0.5250	0.5446
s	0.7	0.7	0.7
Mean $\hat{s}$	0.6996	0.7079	0.7221
Predicted $\hat{s}$	0.7000	0.7090	0.7225

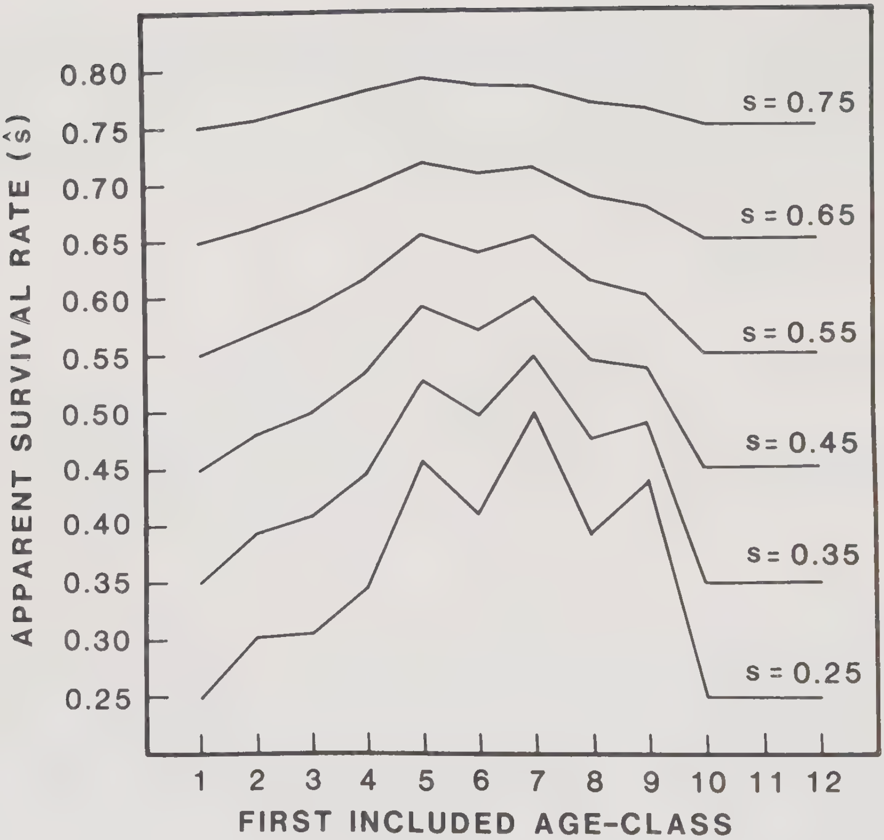

FIG. 1. Apparent survival rates from the C–R method as a function of the first age-class to be included in the estimation. Each line represents a different value of the true survival rate. Errors in age determination are as given in Table 1.

function. It is somewhat fortuitous that the C–R estimator is robust to such changes (if errors are unbiased and all age-classes are included). In the example used here, the method was also unbiased for age-classes 10 and greater. This age is the greatest possible "apparent" age corresponding to the true age at which aging precision becomes constant (Table 1). The C–R method is thus also unbiased in cases where aging precision does not vary with age.

The implications of these results go far beyond the simple examples given here. From information presented thus far, it would seem obvious that bias can be avoided by using the C–R estimator and including all age-classes for which age determination is imprecise. Unfortunately, this solution has a greater conceptual than practical value.

The C–R survival estimator is valid only in the special case where survival rates are constant with age. The decision to use this method is typically based on whether the observed age frequencies fit an expected geometric series age distribution. Robson and Chapman (1961) have formulated a stepwise test that allows the elimination of age-classes that do not meet this expectation. One problem is that errors in age estimation change the shape of the observed age–frequency distribution. Although the true age distribution of a sample may follow a geometric series, the observed distribution may be significantly different, and thus might result in a decision not to use the C–R method or to erroneously eliminate the first age-class(es).

To demonstrate this, Monte Carlo simulations were again used, with the first age-class being chosen by a stepwise chi-square test (Robson and Chapman 1961). Survival rates of 0.3, 0.5, and 0.7 were used, a simulated sample of 1000 aged individuals was drawn, and random errors were introduced in age estimates as before. Using the method of Robson and Chapman to determine the first age-class to be included, mean estimates of survival rates were 0.353, 0.532, and 0.715, respectively, for $s = 0.3$, 0.5, and 0.7, indicating an appreciable positive bias. Ironically, tests that are intended to avoid biases may introduce new biases.

A different problem exists if survival rates change with age: the C–R method is not valid. Most techniques for estimating age-varying survival rates depend on the slope of an age–frequency curve (Caughley 1966; Siler 1979; Barlow 1982, Chap. 2). Because errors in aging typically affect the shape of the observed age–frequency distributions (hence, their slopes), these methods will be biased even if all age-classes are included.

Bias in survival rate estimation resulting from aging errors is thus a complex problem. A general solution for all methods of survival rate estimation does not exist. For the C–R method, a simple approach can be used to estimate expected bias. This approach can be visualized in Fig. 1. For a given error matrix, ***P***, the true survival rate can be interpolated from this figure if the apparent survival rate and initial age-class are specified.

A similar, but more rigorous approach would be to calculate expected age–frequency distributions for a range of true survival rate values. These true-age distributions are then transformed by ***P*** to give estimated-age distributions. The probabilities that the observed age distribution could have been drawn from each of these estimated-age distributions are calculated, and $\hat{s}$ is estimated as the value corresponding to the transformed age distribution that maximizes this probability.

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Reproductive Seasonality in Pelagic Dolphins (*Stenella* spp.): Implications for Measuring Rates

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ABSTRACT

This paper examines the patterns of reproductive seasonality in two species of dolphin in the eastern tropical Pacific: *Stenella attenuata* and *S. longirostris*. These are the principal species used by tuna purse seiners in locating schools of yellowfin tuna in this area. Birthdate distributions are calculated from the lengths-at-capture of fetuses and calves killed in fishing operations, the dates of capture, and the estimated growth curves for these species. Although births were found to occur at all times of the year, distinct modes could be seen in the distributions. Geographic differences in patterns of seasonality could be distinguished on the basis of the strength of the observed modes, the number of modes, and their timing. The northern stock of *S. attenuata* has a diffuse bimodal pattern in annual reproduction with peaks in spring and autumn. The southern stock of this species has a strong unimodal pattern whose timing corresponds to the spring peak in the northern stock. The eastern spinner form of *S. longirostris* also has a single annual peak in reproduction, between March and June, with regional differences in the timing of this mode. The whitebelly spinner form of *S. longirostris* shows a bimodal pattern with peaks in spring and autumn. These seasonal patterns in reproduction can affect reproductive rate measurements by changing our concept of stock boundaries or by introducing biases due to time of sampling. If the mating season is short, this can also limit the rate at which females can be inseminated after an aborted pregnancy, calf death, or weaning.

INTRODUCTION

This report examines the seasonal patterns of reproduction in pelagic dolphins of the eastern tropical Pacific. Four dolphin stocks are considered: the 'northern offshore' and 'southern offshore' forms of the spotted dolphin (*Stenella attenuata*) and the 'eastern' and 'northern whitebelly' forms of the spinner dolphin (*Stenella longirostris*) (see Perrin (1975) and Perrin, Sloan and Henderson (1979) for stock delineations). Stock boundaries for these species are given in Smith (1979); Figs 1, 2, and 3 show approximate ranges. A statistical method is presented for comparing distributions of birthdate, and this method is used to test geographic differences in birthdate distributions within the same species.

S. attenuata and *S. longirostris* are the principal species used by tuna purse-seiners in locating schools of yellowfin tuna. Historical kills of dolphins incidental to this fishery have been large, totaling several millions (Smith, 1979), which has prompted management efforts in recent years. This paper will also consider the implications of seasonal reproduction in measuring the reproductive rates of Cetacea. These implications may prove important in the management of eastern Pacific dolphin stocks.

Previous work on reproductive patterns of these dolphin stocks has shown two broad peaks in calving (one in spring and one in autumn) for spotted dolphins (Perrin, Coe and Zweifel, 1976) and a rather diffuse pattern of seasonality for eastern spinners (Perrin, Holts and Miller, 1977). Perrin *et al.* (1977) found one birth mode in late January of 1974 for eastern spinners, but noted that the timing of births appeared to vary from one area to another. Work on a different stock of *S. attenuata* off the coast of Japan indicated perhaps three peak periods of parturition (Kasuya, Miyazaki and Dawbin, 1974). Similarly Miyazaki (1977) interpreted data on a closely related species (*S. coeruleoalba*) as indicating three annual modes in births.

Of the small toothed whales, strong patterns of reproductive seasonality are most evident in the temperate and subarctic species. The common porpoise (*Phocoena phocoena*) in the North Atlantic (Fisher and Harrison, 1970), the common dolphin (*Delphinus delphis*) off California's coast (Harrison, Boice and Brownell, 1969), the white whale (*Delphinapterus leucas*) off Baffin Island (Brodie, 1971) and the white-sided dolphin (*Lagenorhynchus obliquidens*) off California (Harrison *et al.*, 1969) all show a single period of parturition during the year. Tropical species such as *S. attenuata* and *S. longirostris* and more cosmopolitan species such as *Tursiops truncatus* (Harrison and Ridgway, 1971) may have multiple breeding seasons or diffuse patterns of reproductive seasonality.

MATERIALS AND METHODS

The data upon which this report is based were gathered between 1968 and 1978 by the National Marine Fisheries Service (NMFS) scientific technicians aboard tuna purse-seiners. The sample represents dolphins that were killed as a result of the tuna purse-seining operations. Seining for yellowfin tuna was seasonal during these years, both in its intensity and its areas of operation. Typically, the US fleet concentrated its effort near the coastline for the first several months of the year. Later in the year, fishing intensity slackened and the fleet's efforts were concentrated more offshore.

Extensive life history data were gathered by the NMFS technicians. The items of principal interest in this report were the date, lengths, and collection localities of young dolphins and fetuses that died in the purse seines.

Patterns of reproductive seasonality are most easily summarized by the frequency distribution of birthdates. Two methods were used to estimate birthdates, one from prenatal dolphins and the other from postnatal. These methods are similar to those used by Kasuya *et al.* (1974) and Perrin *et al.* (1976).

Table 1

Postnatal and fetal growth rates used in the projection of birthdate distributions. Postnatal growth parameters are as defined by Perrin *et al.* (1976)

Population	Length at birth (cm)	Postnatal growth parameters a	Postnatal growth parameters α	Fetal growth rate (cm/month)	Reference
Offshore spotted dolphin	82	0.963	1.414	8.28	Perrin *et al.* (1976)
Eastern spinner dolphin	77	0.995	1.365	8.37	Perrin *et al.* (1977)
Whitebelly spinner dolphin	77	0.950	1.290	8.37	Perrin and Henderson (1979)

The first method involves the forward projection of birthdates from fetal lengths and dates of capture. Fetal growth parameters were taken from Perrin *et al.* (1976, 1977) (Table 1). The fetal growth rate of the whitebelly spinner dolphin was assumed to be the same as its conspecific, the eastern spinner; likewise the fetal growth rate of the southern offshore spotted dolphin was taken to be the same as that of the northern offshore spotted dolphin. Only fetuses greater than 10 cm long were used, and growth rates were assumed to be constant. If gestation were significantly less than 1 year, seasonality in sampling could affect the birthdate distributions projected by this method. Since gestation is estimated to be 11.5 and 10.6 months respectively for *S. attenuata* and *S. longirostris* (Perrin *et al.*, 1976, 1977), this effect should be insignificant. No correction was made for the time of sampling.

The second method involves the back projection of the birthdates of postnatal dolphins from their lengths and dates of capture. Postnatal growth rates were taken from Perrin *et al.* (1976, 1977) and Perrin and Henderson (1979). Growth was assumed to follow the Laird/Gompertz model (Laird, 1966).

$$L(t) = L_0 \cdot \exp[(a/\alpha)\cdot(1-\exp(-\alpha\cdot t))].$$

The values used for the parameters above are given in Table 1. These values correspond to the hypothesized 2.0, 1.5, and 1.36 dentinal growth layers in the first year respectively for spotted dolphins (Perrin *et al.*, 1976), eastern spinner dolphins (Perrin *et al.*, 1977), and whitebelly spinner dolphins (Perrin and Henderson, 1979).

The back-projection method was only applied to animals estimated to be less than 1 year old (less than 132 cm for *S. longirostris* and 138 cm for *S. attenuata*). In practice, this method is only useful for young animals, for which growth is rapid relative to individual variation in growth rate. The 1-year age interval was chosen to minimize the potential bias from seasonality in sampling.

Statistical methods used for comparing birthdate distributions are a variation of the Kolmogorov/Smirnov (K/S) one- and two-sample tests. These are nonparametric tests for goodness of fit based on cumulative distributions. Birthdate distributions are, however, circular (Fig. 4), and therefore the results of a conventional K/S test could depend on which month is taken as the beginning of the distribution. The modifications made by Kuiper (1960) and discussed by Batschelet (1965) allow the unambiguous use of these tests on circular distributions. The statistic used for the one sample test is the sum of the maximum positive and negative deviations of the observed cumulative distribu-

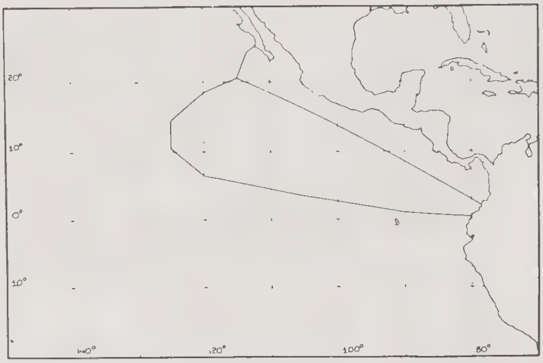

Fig. 1. Geographic distribution of eastern spinner dolphins (*Stenella longirostris*) in the eastern tropical Pacific. Inshore/offshore regions are defined by diagonal line.

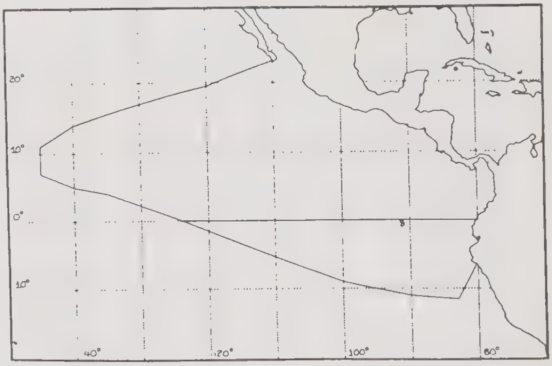

Fig. 2. Geographic distribution of offshore spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific. Northern and southern regions are defined by the equator.

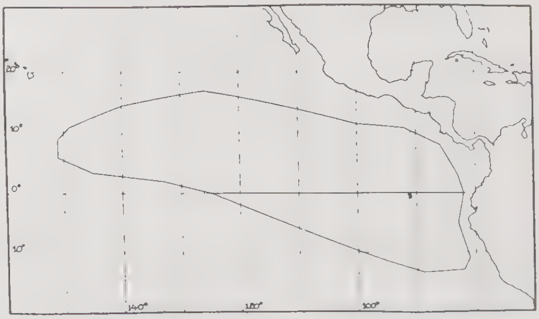

Fig. 3. Geographic distribution of whitebelly spinner dolphins (*Stenella longirostris*) in the eastern tropical Pacific. Northern and southern regions are defined by the equator.

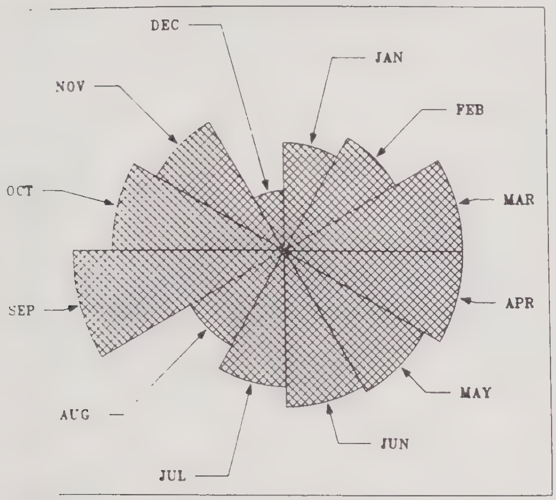

Fig. 4. Birthdate distribution of northern offshore spotted dolphins (*Stenella attenuata*) projected from lengths of fetuses. Length of each ray is proportional to the number of births expected in the given month.

tion from the expected cumulative distribution. Similarly, the statistic for the two sample test is the sum of the maximum positive and negative deviations of one cumulative distribution from the other. The critical values for the two-sample version of this test have not been tabulated for unequal sample sizes. For this reason, statistical comparisons were made only when sample sizes were roughly equal, and in such cases, the smaller sample size was used, which makes the test conservative.

To examine geographic variability in birthdate distributions, where sample size permitted, the samples were stratified by geographical areas. Because Perrin *et al.* (1977) noted an inshore/offshore difference in seasonality for the eastern spinner dolphin, this stock was divided into inshore and offshore ranges by a line drawn roughly parallel to the coastline (Fig. 1). To facilitate statistical comparisons, the line was drawn so as to provide approximately equal sample sizes. The offshore spotted dolphins were divided into a northern and a southern stock by a line drawn along the equator (Fig. 2). In order to better understand the latitudinal variability of reproductive seasonality in this species, the sample of northern spotted dolphins was further divided into those caught between the equator and 5° N and those caught north of 5° N. Due to small sample sizes, geographical stratification of the northern whitebelly spinner range (Fig. 3) was not attempted. Also the southern whitebelly spinner was not considered due to its small sample size.

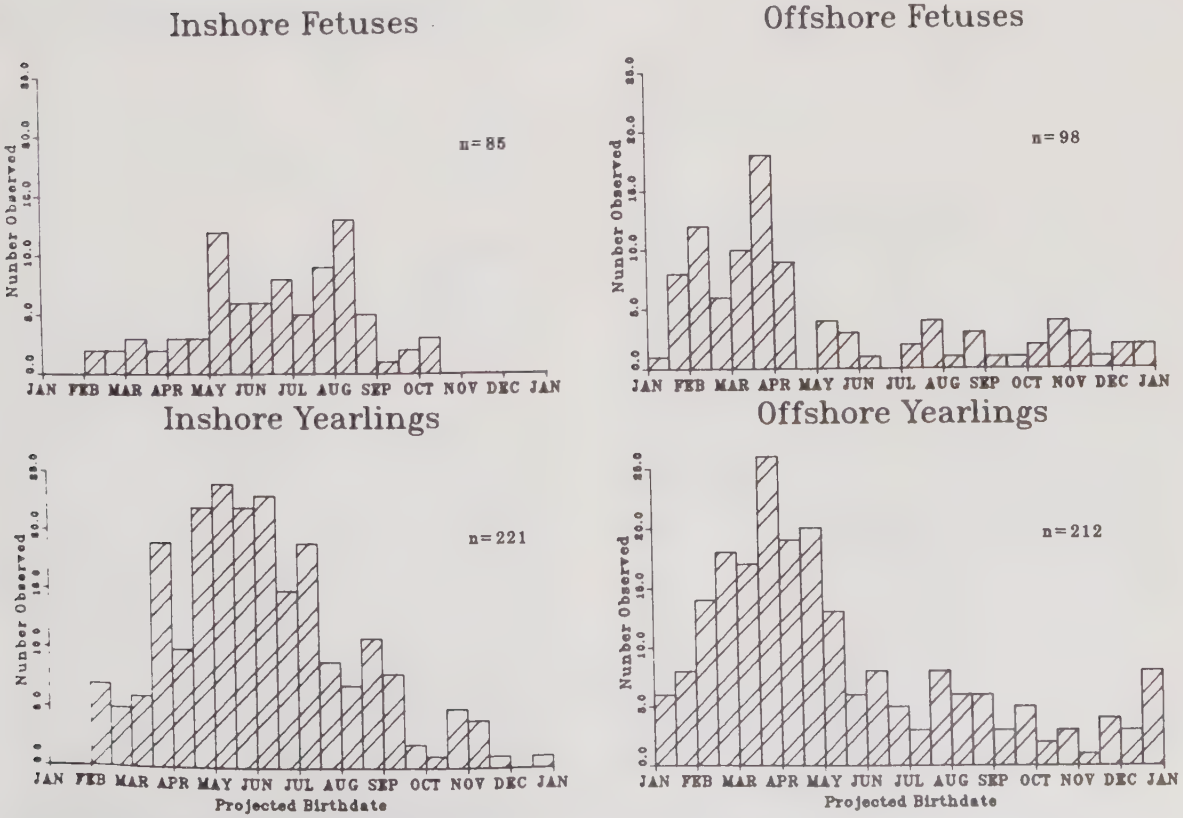

Fig. 5. Birthdate distributions of eastern spinner dolphins (*Stenella longirostris*) projected from lengths of fetuses (top) and calves (bottom). Inshore/offshore geographic stratification is as shown in Fig. 1.

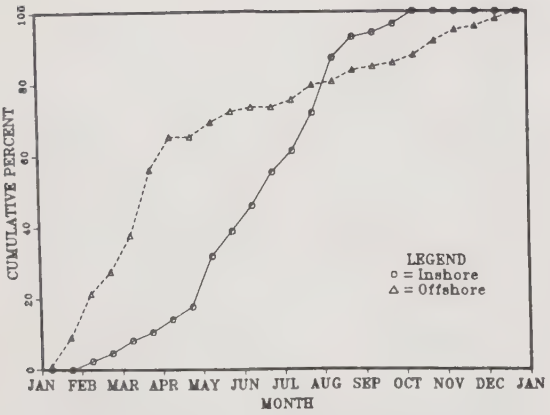

Fig. 6. Cumulative birthdate distributions of inshore and offshore groups of eastern spinner dolphins (*Stenella longirostris*) projected from lengths of fetuses. Geographic stratification is as shown in Fig. 1.

To avoid possible confounding of data for the 'offshore' and 'coastal' forms of the spotted dolphin (Perrin, 1975), only those individuals classified as belonging to the 'offshore' group and found more than 100 km from the coastline were included.

RESULTS

Eastern spinner dolphin

A single, strong peak can be seen in the birthdate distributions projected for the eastern spinner dolphin (Fig. 5). Although similar peaks are evident for both inshore and offshore areas, a regional difference can be noted in the timing of these peaks. For both the forward and back projection methods, the peak calving period occurs earlier in the year for the more offshore group.

The regional differences in seasonality were compared with the two sample K/S test described above (illustrated in Fig. 6 for the projection from fetal lengths). For both projection methods the differences were statistically significant ($P < 0.01$). Although differential growth rates in the two regions could contribute to apparent differences in birthdate distributions, this explanation is unlikely because the forward and back projection methods corroborate each other's results. For growth rate variations to bias the result in the same way for both of the projection methods, the fetal and postnatal growth rates would have to differ in a reciprocal manner. A regional difference in reproductive seasonality is thus indicated for the eastern spinner dolphin.

Whitebelly spinner dolphin

The birthdate distributions for the whitebelly spinner appear to be bimodal when projected from fetal lengths (Fig. 7). The modes are approximately 6 months apart. The birthdate distribution obtained from the lengths of postnatal dolphins shows no evidence of this bimodal pattern (Fig. 7). The two sample K/S test indicates that the two estimated birthdate distributions are significantly different ($P < 0.05$). If a one sample K/S test is applied, the results indicate that the birthdate distribution projected from fetal lengths is significantly different from a uniform birthdate distribution ($P < 0.01$), but that projected from calf lengths is not ($P < 0.1$).

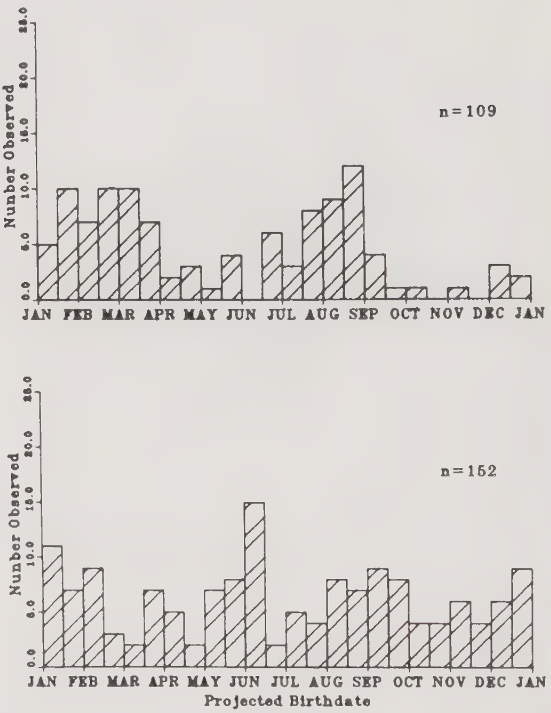

Fig. 7. Birthdate distributions of northern whitebelly spinner dolphins (*Stenella longirostris*) projected from lengths of fetuses (top) and calves (bottom). The equator was taken as the lower limit of their geographic distribution.

Northern offshore spotted dolphin

The birthdate distribution derived from the northern offshore spotted dolphin (Fig. 8) showed a rather even distribution of reproduction throughout the year. Using a one sample K/S test, the observed distributions can be shown to be significantly different from a uniform distribution for both methods of birthdate projection ($P < 0.01$, illustrated in Fig. 9 for projections from fetal lengths). Although the apparent seasonality is not strong, there is a tendency for more births to occur in spring and autumn than in other times of the year. This pattern of seasonality may not be constant from year to year. Perrin *et al.* (1976) suggested that annual changes in the season of peak reproduction might be occurring, and additional evidence for this was presented by Barlow (1979).[1]

Southern offshore spotted dolphin

The distribution of birthdates from the southern stock of the offshore spotted dolphin (Fig. 8) is very different from that of the northern stock of this species. For the southern

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[1] Barlow, J. 1979. Reproductive seasonality in pelagic dolphins of the eastern tropical Pacific. NMFS, Southwest Fisheries Center, Status of the Porpoise Stocks Workshop Doc. 26, La Jolla, California, 27–31 August 22 pp.

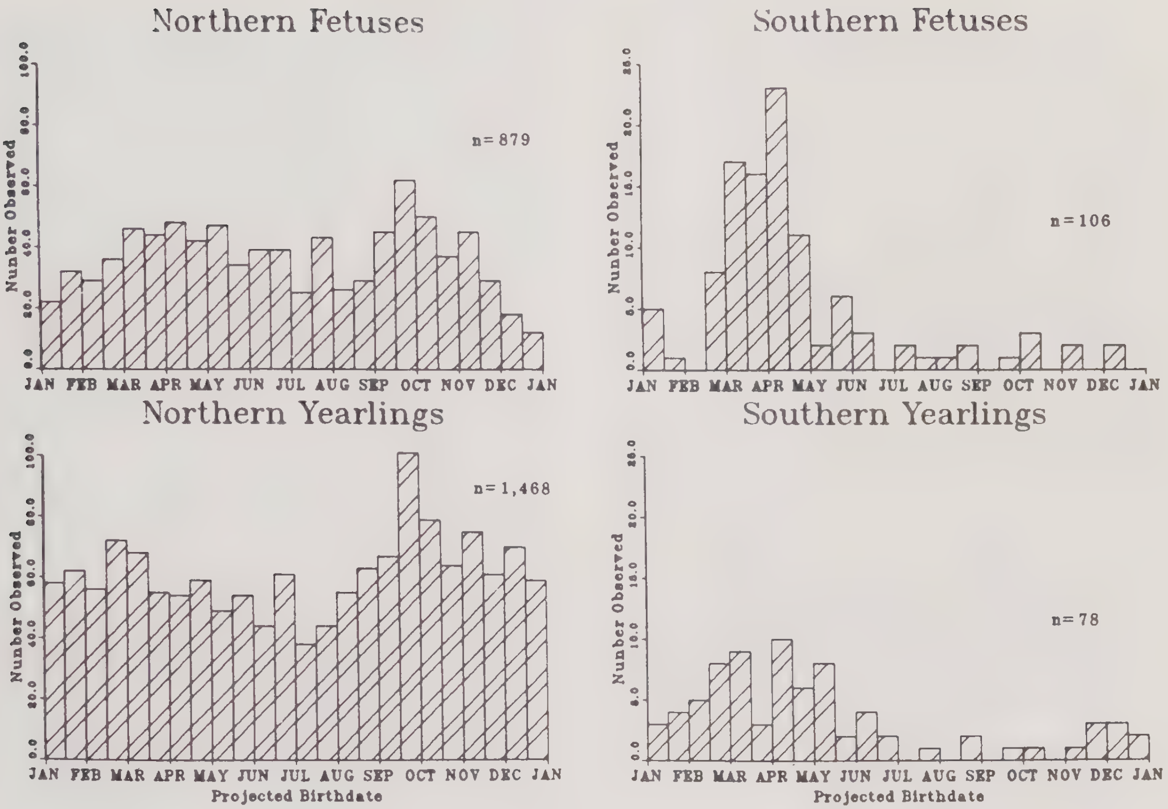

Fig. 8. Birthdate distributions of offshore spotted dolphins (*Stenella attenuata*) projected from lengths of fetuses (top) and calves (bottom). North/south geographic stratification is as shown in Fig. 2.

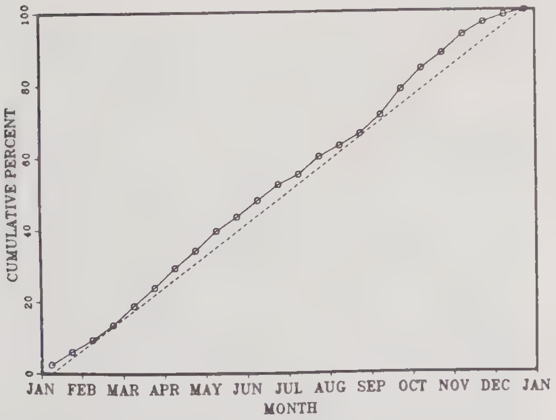

Fig. 9. Cumulative birthdate distribution of northern offshore spotted dolphins (*Stenella attenuata*) projected from lengths of fetuses. Broken line indicates expected cumulative distribution if births were uniformly distributed throughout the year.

stock, the season of parturition is quite short, with most births occurring from March through May. Indeed this group shows the strongest pattern of seasonality of any of the stocks considered here. Sample sizes for the southern population were small, so no attempt was made to divide its range into sub-regions to examine finer geographic differences in birthdates.

Having shown distinct differences between the timing of reproduction in spotted dolphins north and south of the equator, it would be helpful to know whether these changes occur over a narrow range of latitude or whether there is a gradual change from a diffuse bimodal pattern in the north to a strong unimodal pattern in the south. The sample of northern spotted dolphins was therefore stratified into a group taken between the equator and 5° N and a group taken north of 5° N (Fig. 10). Although the sample size is small, those spotted dolphins caught between 0–5° N appear to have a diffuse pattern of seasonality but with one peak from March to June. Two sample K/S tests show this pattern to be significantly different from both that taken from south of the equator (Fig. 8) and that taken from north of 5° N (Fig. 10).

DISCUSSION

As with other dolphin species that have been studied to date, the stocks of *Stenella attenuata* and *S. longirostris* in the eastern tropical Pacific show seasonal patterns in their reproduction. Unlike the strict seasonality of temperate and subarctic species, seasonality in these tropical dolphins is manifest as one or more calving peaks per year, with some parturition occurring throughout the

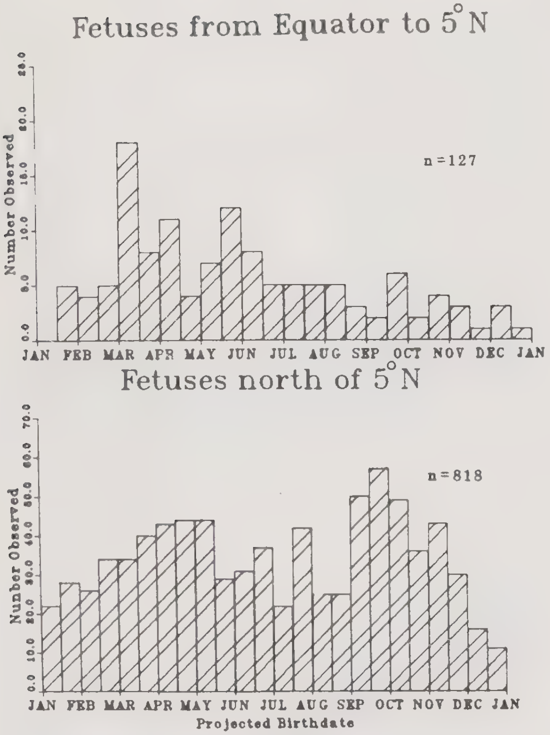

Fig. 10. Birthdate distributions projected from fetuses of northern spotted dolphins (*Stenella attenuata*) grouped by latitude at time of capture.

year. The reproductive seasonality of these species can be characterized by the strength of the observed modes, the number of modes, and their timing. Based on these criteria, there are significant differences in reproductive patterns between dolphin populations that have previously been identified based on morphological criteria, and there is evidence of significant geographic differences in seasonality within these recognized stocks.

The eastern and whitebelly stocks of *S. longirostris* were originally separated on the basis of morphology (Perrin, 1975). This distinction is corroborated by the differences noted here in reproductive seasonality. The eastern spinner (Fig. 5) has a single peak in births, and the whitebelly spinner (Fig. 7) shows at least two modes. It should be noted that the modes in both cases show a sharper definition when projected from fetus lengths. This may attest to the greater precision of the fetal birthdate projection method (despite smaller sample sizes). This would be expected if fetal growth shows less individual variability than that of postnatal animals, or if the estimated growth curves are more accurate for fetuses than for calves.

Within the eastern group, additional geographic differences in seasonality (discussed above) may indicate that a further subdivision of this species would be meaningful. Although both the inshore and offshore groups of eastern spinners show a single annual mode in parturition, this mode occurs significantly earlier in the offshore area. Distributional studies of these dolphins indicate that there are inshore and offshore population centers for eastern spinners with a paucity of sightings in between (Fig. 5 in Au, Perryman and Perrin, 1979). These two observations suggest that the eastern spinner stock might consist of two populations. Regional differences in the timing of a reproductive cycle could be due, of course, to local differences in the seasonality of environmental factors, such as food supply. If this were the case for eastern spinners, reproductive isolation of the inshore and offshore groups would not necessarily result. Before these groups could be identified as separate stocks, further work would be required to determine the degree of isolation, perhaps by means of tagging, genetic, or morphometric studies.

The patterns of seasonality in the northern whitebelly spinner are more difficult to interpret. Although the birthdate distribution projected from fetuses shows a bimodal pattern, that projected from calf lengths shows no clear pattern at all (Fig. 7). Perrin and Henderson (1979) showed that for whitebelly spinners, variations in male testis weight were seasonal, with two modes. The peak periods of testis weight correspond well to the expected breeding seasons given the birthdate distributions taken from fetuses. As noted above, the birthdate distributions taken from fetuses tend to show better definition than those estimated from calves. For these reasons, two annual peaks in reproduction are taken to be the most likely pattern. The absence of these modes in the birthdate distributions projected from calves may be simply due to the combination of sampling error and the high degree of variance associated with this projection method. Alternatively, the difference could be due to misidentification of calves to stock in the area of overlap with the eastern spinner dolphin, or to error in estimating length at birth or postnatal growth rate for this stock. Larger sample sizes may help resolve this apparent discrepancy.

The offshore spotted dolphins were originally considered a single population (Perrin, 1975); however, more recent evidence (Perrin *et al.*, 1979) has supported the consideration of a separate population south of the equator. Evidence presented here for marked seasonal differences in reproduction supports this view. The transition from a diffuse bimodal pattern in the north to a strong unimodal pattern in the south may not be abrupt. Dolphins taken between the equator and 5° N show a single mode synchronous with that of the animals to the south, but they show a more diffuse pattern of seasonality similar to that of the northern spotted dolphins. The explanation of this gradual change is not known. If seasonality in reproduction is determined by the timing of oceanographic or trophic factors, the change could reflect a geographical change in the timing of these physical determinants. Alternatively, the area between 0° and 5° N could represent an area where two separate populations can both occur with the birthdate distribution from that area being a composite of two different distributions. A hiatus in spotted dolphin sightings has been used to determine the boundary between the northern and southern stocks; this region is just south of the equator (Perrin *et al.*, 1979). If this proves to be an accurate boundary, the latter hypothesis could be rejected.

Seasonal patterns of reproduction have been examined for the populations of *Stenella* off the coast of Japan.

Three annual periods of parturition were shown for both *S. attenuata* (Kasuya, Miyazaki and Dawbin, 1974) and *S. coeruleoalba* (Miyazaki, 1977). These estimates were based, however, on the back calculation of birthdates from animals that were up to 2 years old. Individual variation in growth would almost certainly act to obscure seasonal patterns estimated from the older animals. Using only the birthdate distributions taken from fetuses, the data indicate a single mode in the births of *S. attenuata* (Fig. 33 in Kasuya *et al.*, 1974) and an obvious bimodal pattern for *S. coeruleoalba* (Fig. 16 in Miyazaki, 1977).

The reason for the observed differences in reproductive seasonality within the genus *Stenella* are not clear. One possible explanation is that density-dependent changes occurred as a result of exploitation. The southern spotted form of *S. attenuata* has been exploited only lightly (Smith, 1979). This population shows a single strong peak in reproduction, which I will, for purpose of discussion, assume to be the 'natural state' for this genus. Given that all mating occurs at the same time each year, the calving cycle must be an integral number of years: say, for example, 3 years. As exploitation decreases population size, the calving interval might decrease to 2.5 years due to density-compensatory effects. This calving interval would not be consistent with a single annual season of births, hence a bimodal pattern might result. Such a pattern was found in *S. coeruleoalba* off the coast of Japan, in the northern spotted form of *S. attenuata*, and in the northern whitebelly form of *S. longirostris*, all of which have been exposed to moderately heavy exploitation (Kasuya, 1976; Smith, 1979). If the calving period were reduced further, say to 2 years, a single annual mode in births would again be possible. This pattern was seen in the eastern spinner form of *S. longirostris* which has been subject to very heavy exploitation (Smith, 1979). Although speculative, this explanation is consistent with the observed patterns of seasonality in this genus. These predicted patterns can be tested as accurate estimates of calving period become available for these stocks.

Regardless of their cause, the observed patterns of reproductive seasonality can affect our estimation of birth rates for these dolphins in several ways. First, reproductive seasonality, once established, can impose barriers to reproduction and hence change our concept of what constitutes a stock or population. Clearly this is of importance in the management of marine mammals.

Another aspect of seasonality of importance in management is the introduction of bias in the estimation of reproductive rates due to seasonality of sampling effort. For instance, the fraction of pregnant females in a population could be underestimated if sampling of that population were predominantly during the time between the period of peak births and that of peak conceptions. If gestation were 10 months, this time interval would be 2 months. A method for correcting this sort of sampling bias was presented by Barlow (1979). In general, if gestation is close to 1 year (as it is for most dolphins), and if reproductive peaks are somewhat diffuse (as they are for most tropical species), this bias will be small.

The final aspect of reproductive seasonality to be discussed here is a consequence of the synchrony it imposes. If births are restricted to a short season, as in the case of the southern spotted dolphins, then the inter-birth period will necessarily be an integral number of years. This does not mean that the average calving period will be an integer since some individual variability may exist in lactation times and since not all females may become pregnant during the first breeding season after weaning. For birth rate estimates that only involve mean calving interval, synchrony need not affect the resulting estimate of birth rate. However, if the estimation of reproductive rates involve more mechanistic considerations (such as spontaneous abortions and calf mortality) the rate at which females become reinseminated becomes important. If, as was shown by Perrin and Henderson (1979), male fertility is also seasonal, a female that loses her calf might not become pregnant again until the next breeding season. This simple scenario is complicated by the fact that some males always have active sperm production and that conception can occur at any time of the year. Regardless, a model could be developed that would take such seasonal effects into consideration.

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Abrasive Effects of Mount Saint Helens Ash Upon Epidermis of Yolk Sac Larvae of Pacific Herring *Clupea harengus pallasi*

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ABSTRACT

Larval Pacific herring Clupea harengus pallasi *were exposed for 24 h to suspensions of estuarine sediment and volcanic ash from 0 to 8000 mg/litre. The effects of these suspensions on the epidermis of the yolk sac larvae were determined using light and scanning electron microscopy. Examination of the epidermis at specific locations on dorsal and ventral body surfaces showed that the effects were apparent with increasing concentrations of both sediment and ash. The effects of volcanic ash, however, occurred at lower concentrations and were of greater magnitude than those of sediment. Examination of the epidermis of these larvae under the scanning electron microscope revealed puncture-type damage associated with volcanic ash but not estuarine sediment. Thus, in addition to the possible effects of smothering which may occur with fine particulates, the ash particles result in direct mechanical damage to the delicate early larvae. The concentrations where effects were noted were greater than those likely to be observed in the lower Columbia River estuary where the larval herring occur. In upriver locations characterized by higher suspended particulates, delicate larvae of other species may suffer epidermal damage.*

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INTRODUCTION

The eruption of Mount Saint Helens had far-reaching effects on aquatic resources from the headwaters of the Toutle River to the Columbia River estuary, and was even noted offshore in the Columbia River plume waters (Baker & Curl, 1981). Virtually all of the fish in the Toutle River, and the Cowlitz River below its confluence with the Toutle, were killed (Martin *et al.*, 1982). Shoals of ash and mud up to 7·6 m deep were found in the Columbia River; these deposits have also been carried to the estuary where shoaling has been noted near the port of Astoria. Some 10·7 million cubic yards of sediment would have to be dredged to return the river to its original dimensions. Dredging may increase particulate loads in downstream locations and impact fishes. Resultant sedimentation and higher suspended particulate loads may alter the fishes' physiology (Redding & Schreck, 1982), behavior (Gardner, 1981; Swensen & Matson, 1976), and have other effects (Muncy *et al.*, 1979). These effects may affect fishes of the lower Columbia River estuary, a nursery area for many marine fish species (Misitano, 1977); increased sedimentation rates may affect reproduction, hatching and larval survival, as has been noted in other habitats (see Muncy *et al.*, 1979 for a review). Ash particles may have further detrimental effects on epidermal and gill tissues of fishes; more devastating effects might occur in delicate tissues of early larvae, which are more susceptible to sublethal effects than are later life stages.

The effects of suspended ash upon fish larvae have not been studied; research studies on salmonids began almost immediately after the eruption, but the results are not completely clear. The Toutle and Cowlitz River system had large runs of economically important salmonids before the volcanic eruption. The immediate effect on these fish was devastating, as shown by live box bioassays, but lethal effects may have resulted from stresses other than suspended particulates alone (Stober *et al.*, 1982). Other sublethal effects of volcanic ash have also been examined in salmonids. Volcanic ash is composed primarily of silica (Fruchter *et al.*, 1980), that has sharp, angular characteristics which might enhance abrasion. Although early reports detected abrasion and puncturing damage by ash particles from fish in live boxes (T. Yasutake, pers. comm.), Stober *et al.* (1982) found no effect of suspended ash on the structure of gill tissue or upon the subsequent ability of smolts to enter seawater or perform in swimming trials. Under short-term conditions, Redding & Schreck (1982) also found no mechanical abrasion of the gills.

Volcanic ash may nonetheless lower the chances of subsequent survival of fish, and its sublethal effects may become more pronounced when other stressful factors, such as increased water temperature or velocity, are evident.

We know that survival of the egg and larval stages of marine fishes is important to population dynamics; it has been suggested that critical periods of heightened mortality at these stages may result in the determination of year class strength (Hjort, 1914; Hunter, 1976). While some factors may be severe enough to cause larval mortalities, sublethal stresses have important effects upon fish eggs and larvae (Rosenthal & Alderdice, 1976).

The overall goals of this research are to determine the abrasive effects of suspended ash and estuarine sediment on the epidermis of larval Pacific herring, *Clupea harengus pallasi*—a marine species which spawns in the lower Columbia River estuary. This species has adhesive, demersal eggs, a common characteristic among estuarine-spawning fishes. It is an important resource in the northern Pacific, both as a commercial catch and as forage for other important species.

MATERIALS AND METHODS

The preparation of volcanic ash and estuarine sediment for these experiments is described in Boehlert & Morgan (in preparation). Particles larger than 24 μm were removed by settling over a 10 cm water column. This resulted in a particle size distribution smaller than that used in other experimental studies (Stober *et al.*, 1982; Redding & Schreck, 1982), but was necessary in order to maintain suspensions for the work on fish larvae. Final particle sizes of volcanic ash and estuarine sediment were analyzed with a Coulter®* counter and were slightly different, with 96 % (by weight) of both ash and sediment between 3 and 19 μm.

Experiments were designed to evaluate the effects of suspended sediment and ash on the epidermis of newly hatched herring larvae. The experiments were carried out on 19–20 March, 1982 with eggs which had been spawned naturally on the north jetty of Yaquina Bay. All eggs and larvae were maintained in seawater adjusted to 15‰ salinity at 10 °C. After hatching, groups of 20 larvae were placed in individual 1-litre containers held within 10-litre tanks. The 1-litre containers had a 335 μm nylon mesh bottom to allow free flow of sediment and ash suspensions. Larvae were introduced into duplicate containers at six levels of suspended ash or sediment (0, 500, 1000, 2000, 4000 and 8000 mg/litre). Each 2 h the suspension was replaced with a new 1-litre volume slowly siphoned into the vessel. Over the 2-h interval, the ash and sediment concentrations decreased through settling to approximately 25 % of the initial values. After 24 h, the larvae were removed to petri dishes and enumerated as either dead or alive, based upon presence or absence of heartbeat. Live larvae were subsequently preserved for later microscopic analysis in 2 % buffered glutaraldehyde in teleost saline.

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* Coulter® is a registered trade name of Coulter Electronics Inc., Hialeah, USA.

Preserved larvae were randomly selected and subsequently processed for histological analysis following the techniques of O'Connell (1976) and serially sectioned at 6 μm on a rotary microtome. Sections were mounted on glass slides and stained with Harris' hematoxylin and eosin-phloxine B. Sectioned specimens were examined under a microscope for evidence of abrasion to the epidermis in yolk sac experiments. All larvae were identified with random numbers and were examined without knowledge of the experimental treatment. Two areas were chosen for detailed histological analysis of epidermal structure. The first was the epidermis on the ventral surface of the yolk sac, the second the epidermis on the dorsal surface in the region of the nape, just posterior to the head. In serial sections from each larvae, four sections from the areas of interest were randomly chosen and examined at 1000 magnification. Each of these sections was graded on a qualitative basis from 1 (good, characteristic of normal fish) to 3 (poor, characterizing severely abraded epidermis). The criteria for these assessments are as follows:

1. Good, epidermis smooth at surface, characterized by some small protrusions. Occasional eosinophilic vesicles, particularly in the ventral region. No separation of epidermis from underlying tissues or shrinkage apparent (Fig. 1D).
2. Intermediate, epidermis smooth to slightly abraded, with thin, irregular eosinophilic processes differing from the protrusions noted above. Some separation of epidermis from underlying tissues.
3. Poor, external surface of epidermis rough, with apparent abrasion and epidermal puncturing. Frequent separation of epidermis from underlying tissues (Fig. 1, E and F).

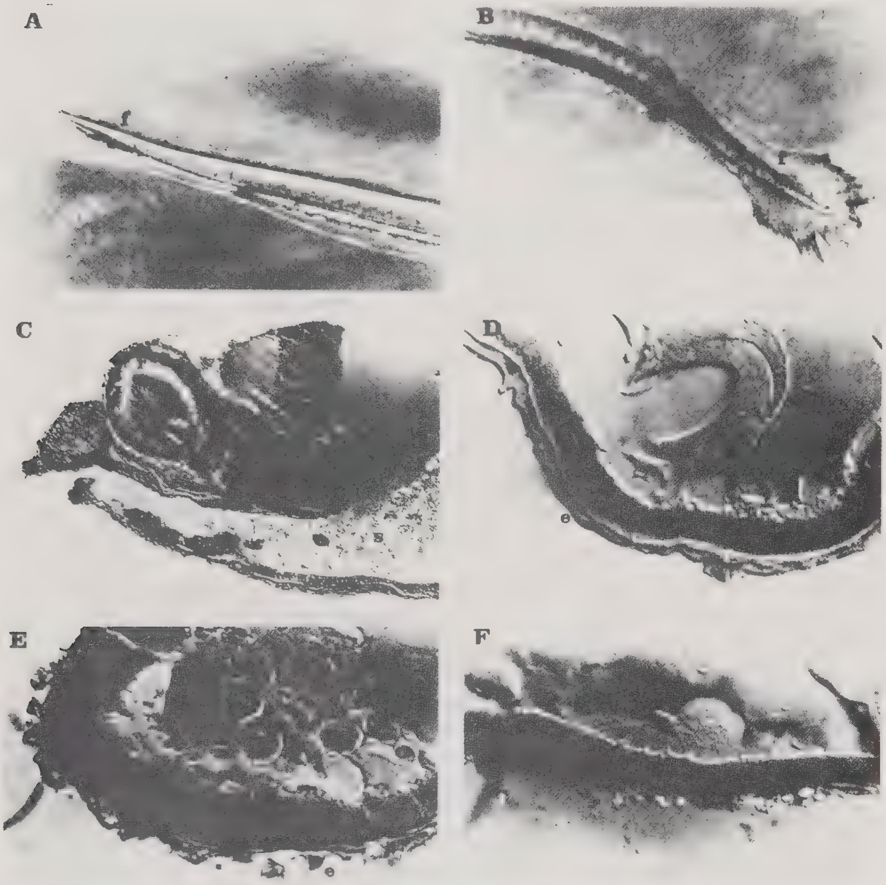


Fig. 1. Photomicrographs of the epidermis and finfold of yolk sac larval *Clupea harengus pallasi* exposed to various concentrations of ash or sediment for 24 h. A. Caudal region from a larva in the control. The finfold is generally intact with the exception of minor damage to the most posterior region. B. Caudal region from a larva exposed to 2000 mg/litre volcanic ash. Note the irregular nature of the finfold and the abrasion to the margin, particularly on the caudal finfold. C. Head region of a larva from the 1000 mg/litre sediment exposure. Note the sediment particles in the gullet; the gut in this yolk sac larva is not yet open (720 ×). D. Epidermis in the yolk sac region of a larva exposed to 2000 mg/litre sediment. The epidermis is smooth and uniform and was graded as condition 1 (cross-section, 3500 ×). E. Epidermis in the yolk sac region of a larva exposed to 4000 mg/litre sediment. The epidermis was graded as condition 3 (poor). Note the deterioration and rough surface (cross-section, 2200 ×). F. Epidermis from the yolk sac region of larva exposed to 8000 mg/litre volcanic ash. The epidermis was graded as condition 3 (poor); it is discontinuous and abraded (longitudinal section, 2200 ×). e, epidermis; y, yolk mass; s, sediment particles; f, finfold; r, retina.

While examining these histological sections, care was taken to ignore damage from histological procedures, which was occasionally present as section fracturing; this was particularly apparent on the yolk sac epidermis, where the brittle yolk is difficult to section smoothly. After the four sections were examined from each specimen and the condition assigned, a mean value for each area was determined. The mean of these mean values for a number of specimens is presented as the value for a given ash or sediment concentration of suspensions. Within areas and treatments, the effects of concentration were determined with one-way analysis of variance.

Specimens were also prepared for scanning electron microscopy. Larvae were prepared for observation following the procedures of Dobbs (1974). Briefly, larvae were preserved in 2% glutaraldehyde, dehydrated through a graded series of alcohols, and put in two changes of liquid freon. Larvae were placed in small porous capsules and processed in a critical point dryer. They were mounted on studs using double stick tape and coated with a thin layer of gold–palladium in a vacuum evaporator. These specimens were examined on an AMR 1000 scanning electron microscope. Particular attention was paid to the epidermal tissues and the presence of ash- or sediment-related damage.

RESULTS

Larvae generally appeared to be in worse condition in the higher concentrations of ash. This assessment was based upon condition of finfold and probable epidermal damage observed under the dissecting microscope. While finfolds in sediment often had adhering particles, they were not abraded as in higher ash concentrations (Fig. 1, A and B).

Mean mortality rates over all concentrations, including controls, were 5·40% (SE 1·65%) for ash and 5·28% (SE 2·35%) for sediment. No differences in mortality were apparent between controls and the suspensions of ash and sediment at the end of the 24-h exposures, despite an apparent difference in the epidermal condition of larvae (Fig. 1, A and B). Larvae were not maintained beyond the 24 h period, however, to evaluate sublethal stress and possible subsequent mortality. In examination of the histological preparations, about 65% of the scores within sections agreed. Mean scores showed a general trend of increase with increasing ash or sediment concentration in both dorsal and ventral

TABLE 1

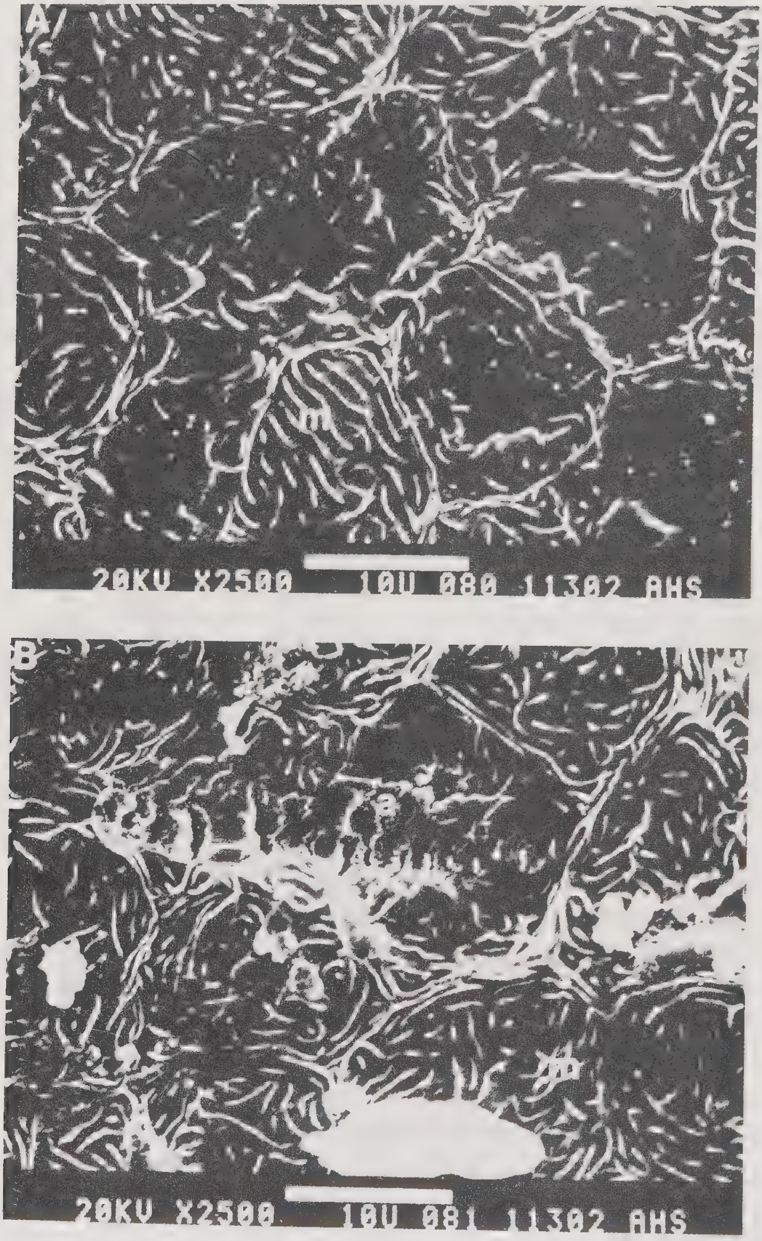
Histological Assessment of Epidermal Structure in Larval Pacific Herring[a]

Region	*Concentration* (*mg/litre*)	*Volcanic ash* *N*	$\bar{X}$	*s*	*Estuarine sediment* *N*	$\bar{X}$	*s*
A. Ventral yolk sac	0	10	1·35	0·36	10	1·35	0·36
	500	5	1·75	0·56	4	1·25	0·20
	1 000	5	1·90	0·52	3	1·33	0·14
	2 000	6	2·00*	0·72	3	1·42	0·29
	4 000	6	1·96*	0·56	5	1·65	0·65
	8 000	6	2·03*	0·49	4	1·63	0·32
B. Dorsal nape	0	9	1·11	0·13	9	1·11	0·13
	500	3	1·25	0·25	4	1·13	0·14
	1 000	5	1·65*	0·29	3	1·33	0·14
	2 000	3	1·83*	0·29	3	1·25	0·25
	4 000	6	1·96*	0·19	5	1·45*	0·21
	8 000	5	1·87*	0·31	3	1·75*	0·25

[a] Four sections of epidermis on each specimen were graded on a subjective scale of 1 (good) to 3 (poor) for dorsal surface and ventral yolk sac regions. Values in the Table represent the mean value in each treatment. Experiments were run concurrently and controls were combined. Asterisks indicate treatment means significantly different from the appropriate controls (ANOVA, LSD, $P < 0·05$). *N*, number of specimens; $\bar{X}$, mean ranking; s, standard deviation.

epidermal areas (Table 1). In the controls, the mean score was better for the dorsal than the ventral (yolk sac) region. For the ventral epidermis, there were no significant effects of increasing sediment concentration on epidermal structure, whereas effects were noted due to volcanic ash exposure with significant mean scores at suspensions greater than 2000 mg/litre. In the dorsal nape region, greater effects were noted for both estuarine sediment and volcanic ash. Controls were significantly different from the sediment concentrations of 4000 and 8000 mg/litre, and from all ash concentrations of 1000 mg/litre and greater (Table 1). Since the same controls were considered for both ash and sediment, the abrasive effects of ash were greater than those of sediment.

Observations with the scanning electron microscope are in general concurrence with the histological observations. Observations of the lateral epidermis of control yolk sac larvae show structures typical of developing teleost epidermis (Roberts *et al.*, 1973), with distinct cellular borders and microridges (Fig. 2A). Small, irregular particles, possibly associated with the processing, were occasionally apparent. The margins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m
20KV X2500 10U 080 11302 AHS
B
a
p
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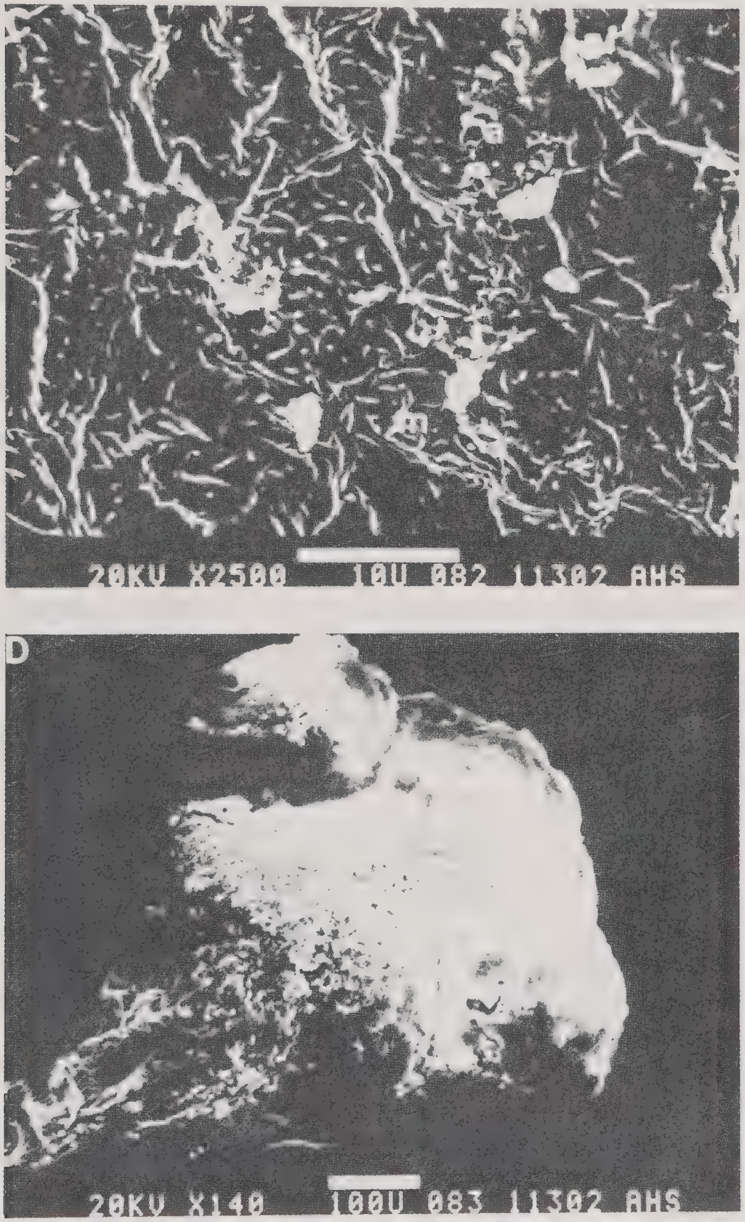
Fig. 2. Scanning electron micrographs of the epidermis from yolk sac larvae of Pacific herring exposed to ash or sediment for 24 h. A. Control larva. Normal epidermis on the lateral body surface near mid-body. Microridges and cell boundaries are distinct. B. Lateral body surface epidermis from a larva exposed to 1000 mg litre volcanic ash. Note the small puncture- and tear-type abrasions and the particles on the body surface.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D
20KV X140 100U 083 11302 AHS

Fig. 2—*contd.*

C. Lateral body surface epidermis from a larva exposed to 8000 mg/litre volcanic ash. The small tears are apparent, as are ash particles. D. Head region of a larva exposed to 8000 mg/litre estuarine sediment. Note the fine layer of sediment coating the head region. a, abrasive damage to the epidermis; m, epidermal microridges; e, eye; s, sediment particles.

of the finfold were normal. Specimens examined from either ash or sediment suspensions, however, showed moderate to abundant particles on the epidermis. Specific abrasion is apparent in the ash experiments, which results in tear- and puncture-type damage rather than a smooth overall abrasion. Puncture wounds at 1000 mg/litre ash were common over the body surface, ranging in size from about 1 to 5 μm (Fig. 2B). The finfold margins were rough compared with the controls. Similar finfold damage was seen on most larvae in ash suspensions. In larvae from 8000 mg/litre ash, puncture wounds and ash particles were apparent on the lateral epidermis, with possibly embedded ash particles (Fig. 2C). In the higher ash concentrations, the ash particles in many cases comprised a fine coating, particularly on the head region. Groups of particles seemed to be maintained in some kind of coating, possibly mucous. The origin of this material is uncertain, however, as mucous-secreting goblet cells are relatively rare in larval herring epidermis.

In the specimens from estuarine sediment experiments, the puncture-type epidermal damage was not as apparent as in the ash experiments. The epidermis generally appeared similar to that of controls with the exception of less distinct microridges and increasing abundance of particles of sediment on the larvae in the higher concentrations. Again, agglutinated groups of sediment particles were most commonly found on the head region (Fig. 2D). Finfold margins were not roughened, as in the ash trials.

DISCUSSION

Egg, as well as larval, stages of fishes are characterized by heightened sensitivity to stress, pollution and physical factors, as compared with later life history stages (Rosenthal & Alderdice, 1976). Within the egg, developing embryos are subject to a wide variety of stresses including elevated temperature, salinity, heavy metals, ultraviolet radiation, lowered dissolved gases and other factors. The embryonic stages, moreover, may be more sensitive at selected critical periods of development (Vladimirov, 1975), when cytological or genetic damage may occur.

When larvae hatch, they no longer have the protection of the chorion. Hunter (1972) and Weihs (1979) demonstrated that newly hatched northern anchovy *Engraulis mordax* larvae depend upon the epidermis for gaseous exchange, a situation typical of many fish larvae. If larvae develop a coating of particulates over the epidermis, smothering may become a problem for respiratory gas exchange. The epidermis in early larvae, furthermore, is only a few cells thick (O'Connell, 1981; Jones *et al.*, 1966), making larvae subject to abrasion damage and other potentially sublethal effects. Rosenthal (1971) noted that exposure of yolk sac herring larvae to red mud particles resulted in ingestion and potential inability to initiate later feeding. I noted a similar phenomenon of ingestion (Fig. 1C), but later larvae were clearly able to feed (Boehlert & Morgan, in preparation).

Epidermal damage noted on larvae in the suspensions was probably the result of abrasion. Qualitatively, the larval epidermis, as observed at the finfold, was markedly damaged (Fig. 1A). This damage was observed histologically as well (Fig. 1, D through F). While histological damage has been noted in juveniles and adults, no published work shows detrimental effects of sediment or volcanic ash upon histological features of larval fishes. Herbert & Merkens (1961) observed increased healing time for wounds in fish exposed to sediment loads, resulting in higher probability of bacterial infection. Sherk *et al.* (1975) noted a change in the gill structure of white perch exposed to sediments; especially obvious was the increase in the abundance of mucous-producing goblet cells, which presumably aid in removal and sloughing of sediment from the gills. Larvae, however, may lack the ability to remove particles with mucous (Everhart & Duchrow, 1970); indeed, goblet cells are not obvious features of larval herring epidermis and were not abundant under any conditions in the present study. Unpublished findings on the histological changes in yearling chinook salmon exposed *in situ* to volcanic ash suggest marked effects. The epidermis was badly abraded, with approximately one-eighth its normal thickness and loss of all epidermal mucous cells. Pathological conditions were also noted on the gills and pseudobranch, both of which are exposed directly to the ash (T. Yasutake, pers. comm.). This suggests that the sharp glass and crystalline structure of the volcanic ash (Fruchter *et al.*, 1980) may result in cellular and tissue damage greatly beyond that caused by sediment alone.

The results of more recent studies on the histological effects of ash exposure, however, are equivocal. Stober *et al.* (1982) and Redding & Schreck (1982) found no damage to the gill tissue of juvenile salmonids dosed with volcanic ash in the laboratory, despite relatively high dosages. This also points out the differences between effects in the field and laboratory, since Stober *et al.* (1982) also noted significantly higher lethal levels of ash in the laboratory as compared with the live box bioassays in the field shortly after the eruption. The concentrations of suspended ash and sediment were environmentally realistic for some river locations. Dinehart & Culbertson (1982) observed peak concentrations of 99 000 to 400 000 μg/litre in the Toutle River. Values in the lower estuary, while unknown, are doubtless much lower but may vary as activities such as dredging take place. Thus the possibility of epidermal damage does exist in the field.

In summary, histological work on the yolk sac larvae of Pacific herring showed that both dorsal and ventral epidermal tissues were in significantly poorer condition than controls, apparently from abrasion associated with exposure to volcanic ash. Estuarine sediments caused less extensive damage, affecting the dorsal area only. These effects were apparent as frayed finfolds (Fig. 1B) and the poor condition of the epidermis in higher concentrations of sediment and ash. The abrasive damage noted in these specimens under the light microscope (Fig. 1, E and F) correlated with the damage apparent under the scanning electron microscope, where the presence of puncture-type damage to the epidermis of larvae exposed to volcanic ash was apparent (Fig. 2). Since all of the larvae were alive at the time of preservation, the damage noted probably represents a sublethal effect which would probably have resulted in later mortality.

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Scanning Electron Microscopy

G. W. Boehlert

SCANNING electron microscopy is an ideal tool for description of microstructure in taxonomic studies. The scanning electron microscope (SEM) provides a surface image characterized by high resolution and depth of field and a three-dimensional quality unavailable with other techniques. In many cases this allows one to objectively describe microstructure where only subjective descriptions were available in the past. It is the purpose of this contribution to describe the techniques and use of scanning electron microscopy and its application to systematic investigations of fish eggs and larvae.

The SEM has been used in a wide variety of systematic and evolutionary investigations. With available magnifications from 10 to greater than 100,000 times, the SEM covers the range from dissecting and compound light microscopy to transmission electron microscopes. It has thus been immensely important to progress in classification in the study of micropaleontology, botany, insects and mites, and a wide variety of microorganisms, among other taxa (Heywood, 1971; Kormandy, 1975). Taxonomic applications of the SEM to fishes have been more limited. Several studies have used the SEM for studies of morphology, including epidermis, gill tissue, optic capsules, eggs, sperm, and embryos of fishes (Dobbs, 1974, 1975).

Microstructural analysis of otoliths of fishes with the SEM is now common (Pannella, 1980). For early life history stages, the most frequent use in identification and classification has been with the egg stage. The chorion, or external membrane, of many species is variously ornamented with filaments, spines, patterns of ridges, loops, blebs, and pustules (Ahlstrom and Moser, 1980; Robertson, 1981; Matarese and Sandknop, this volume). These ornamentations and the ultrastructure of the chorion are species-specific (Ivankov and Kurdyayeva, 1973; Lonning, 1972). While many of these structures may be easily visualized with light microscopy (Hubbs and Kampa, 1946; Kovalevskaya, 1982), the SEM often provides the best means of adequately describing structures which are very small or transparent under the light microscope. The egg chorion of *Maurolicus muelleri,* for example, was described as "drawn up into hexagonally arranged points," by Robertson (1976) based upon light microscopy but as "drawn up into hexagonal ridges . . . and slightly raised at the point of intersection" under the SEM (Robertson, 1981). Similarly, Boyd and Simmonds (1974), among others, suggested that the chorion of southern populations of *Fundulus heteroclitus* lacked fibrils using light microscopy, whereas the SEM showed the presence of numerous short and thin fibrils (Brummett and Dumont, 1981). Thus for purposes of classification, the SEM allows visualization of surface structures that are difficult to describe with light microscopy.

Methodology

Preparation of biological material for examination under the SEM is concerned with preservation, dehydration, and coating with a conductive material. Fixation of labile biological specimens is necessary because removal of water during the stages of dehydration may result in collapse of cells and other artifacts. Depending upon the method of fixation and dehydration, the artifacts can range from shrinkage to collapse or fracture of the structures to be observed. It is preferable to begin with fresh, live material. For eggs this requires either laboratory spawning or abundant eggs from the field which can be reliably collected. For larvae at different stages, it is difficult without laboratory rearing facilities. Results with formalin-fixed material from plankton collections will generally be satisfactory for lower magnification analysis of surface morphology, but may not reflect the quality of freshly prepared material.

Fresh material should be fixed for electron microscopy. Larval stages may first be relaxed in anesthetant solution (such as MS-222). Initial fixatives for both eggs and larvae are generally based upon glutaraldehyde, with concentrations ranging from 0.5 to 4.0%; lower concentrations are typically followed by post-fixation. A fixative which I have found acceptable is that from Dobbs (1974) as follows: 70% glutaraldehyde—2.0 ml, flounder saline—34 ml, and distilled water—34 ml. The flounder saline follows Forster and Hong (1958) and contains the following (in grams per liter): NaCl, 7.890; KCl, 0.186; $CaCl_2$, 0.167; $MgCl_2 \cdot 6H_2O$, 0.203; $NaH_2PO_4 \cdot H_2O$, 0.069; $NaHCO_3$, 0.84. The fixative has a final osmolarity of 380 mOsm/l. Fixation should be for 24 hours. Other authors provide several other fixatives. One suggested by Stehr and Hawkes (1979), while more difficult to prepare, is also useful should transmission electron microscopy be desired for the same material. Post-fixation in osmium tetroxide is recommended by several authors as a means of hardening particularly soft tissues. Generally, 1–2% osmium tetroxide in buffered saline is used. I have found this unnecessary with fish eggs and larvae, as suggested by Dobbs (1974) and Stehr and Hawkes (1979). It may be considered, however, if collapse is a problem. Lonning and Hagstrom (1975) suggested that egg chorions not post-fixed would rupture under the electron beam; I have not noticed this.

It is the process of dehydration where the greatest artifacts are likely to occur. With larvae, shrinkage of tissue may occur, while eggs may suffer complete collapse. On larger eggs, puncturing the chorion with a sharpened dissecting needle may facilitate transfer of fluids and prevent this collapse (Stehr and Hawkes, 1979).

Removal of water from the tissues is prerequisite to coating and observation, which are both conducted under high vacuum. Two methods are available, freeze drying and critical point drying. For freeze drying, unfixed fresh material may be used. Fixed material should first be rinsed with distilled water to remove salts, and then plunged with little adhering water into liquid nitrogen. Damage here may result from formation of ice crystals if freezing rate is too slow, but this is typically not a problem with small eggs and larvae in liquid nitrogen. Boyde and Wood (1969) recommend using 20 ml chloroform per liter of distilled water to increase nucleation rates and decrease ice crystal formation. After freezing, the material is immediately introduced into the freeze dryer, where water sublimes, leaving the specimen dry and intact. Critical point drying, on the other hand, requires dehydration through a graded series of alcohols (20% for 24 h, then 10–20 min each in 50%, 70%, 80%, 90%, 95%, and two changes of absolute ethanol). The ethanol is then replaced with either freon or acetone depending on whether freon or carbon dioxide critical point dryers are used. The steps of dehydration and transfer can be done in small specimen holders to minimize handling and possible surface damage. After dehydration, specimens must be mounted on SEM studs with any of several available adhesives and tapes. The dried specimens are particularly delicate and should be handled with a small camel-hair brush to avoid damage to the surface. They are then oriented onto the stud under a dissecting microscope. Before coating, no further preparation is necessary with larvae, but eggs have only a small area of electrical contact with the stud. It is therefore advisable to use a conductive adhesive (such as silver paint) to make a more complete electrical connection and prevent charging, which decreases image quality. This paint should be allowed to become tacky prior to positioning the eggs, or it may cover portions of the egg itself. Finally, specimens are coated with a thin conductive layer, typically of gold or gold-palladium, by either vacuum evaporation or ion sputtering, prior to viewing on the SEM. At most facilities, trained SEM technicians are available; their advice and assistance are invaluable and should be sought.

Results and Discussion

Shrinkage and other artifacts will vary depending upon the type of material, preservation, and method of dehydration. For fresh material preserved in a mixture of formalin, glutaraldehyde, and acrolein, Stehr and Hawkes (1979) observed a shrinkage of approximately 10% in the eggs of *Platichthys stellatus* and *Oncorhynchus gorbuscha*; the latter had been punctured prior to dehydration. In the present study, eggs of *Maurolicus muelleri* initially preserved in 5% buffered formalin showed varying degrees of shrinkage and collapse depending upon subsequent treatment. The least shrinkage (12%, Fig. 18B) was noted in material which was freeze dried, whereas post-fixation and dehydration through freon 113 associated with critical point drying resulted in shrinkage of up to 67% of the original diameter (Fig. 18D). Eggs of this species show a hexagonal sculpturing; under the light microscope the sculpturing is hyaline and difficult to interpret (Fig. 18A). Eggs prepared by freeze drying clearly show the surface sculpturing; note particularly the ridges, which are more clearly defined (Fig. 18B). For comparison, an egg which had partially collapsed during dehydration is shown (Fig. 18D). The obvious differences in shrinkage point out the importance of specifying method, initial size, and shrinkage values, particularly for comparative or taxonomic studies.

Eggs from other species are shown to give an idea of the range of chorion structures which may be observed. The hexagonal pattern on *M. muelleri* overlies a highly porous surface structure

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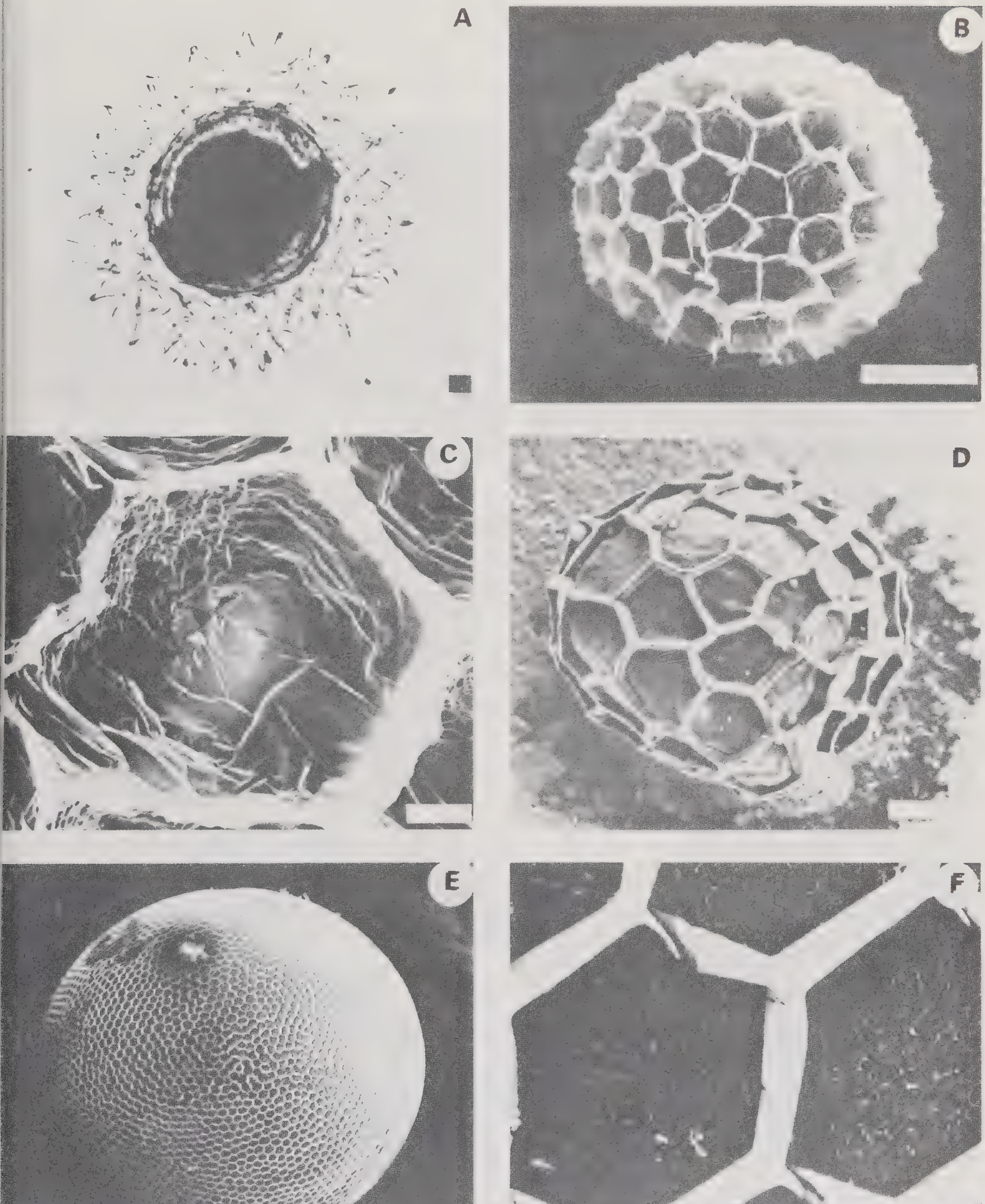
Fig. 18. (A) Egg of *Maurolicus muelleri* from off South Africa taken under the compound light microscope with transmitted, polarized light. Note the emphasis of the points on the hyaline chorion, which represent the intersections of ridges. Bar = 100 μm. (B) Egg of *M. muelleri* under the scanning electron microscope. Note the areas between what one would interpret as points on Figure 18A, which are now seen as polygonal facets or ridges. Bar = 500 μm. (C) Individual facet of the egg of *M. muelleri*. Note the porous and diaphanous nature of the egg surface. Bar = 50 μm. (D) Egg of *M. muelleri* post-fixed in osmium tetroxide and critical point dried. The shrinkage of this specimen is approximately 65%. Note the differences in morphology of the ridges and surface of the egg. Bar = 100 μm. (E) Egg of *Pleuronichthys coenosus*. The facets are relatively small by comparison with *M. muelleri* and the pattern units are more regularly hexagonal. Bar = 100 μm. (F) Detail of two hexagons from the egg of *P. coenosus*. Note the morphological differences between both the ridges and chorion surface as compared to *M. muelleri*. Bar = 10 μm.

Fig. 19. (A) Egg of *Atherinopsis californiensis*. The filaments are single, terminate in loose ends, and are distributed over the entire egg surface. Bar = 1,000 μm. (B) Egg of *Atherinops affinis*. The egg of this species is characterized by filaments which are looped, with no free ends (Curless, 1979). This differentiates it from the egg of *A. californiensis*, as do filament length, abundance, and basal morphology. Closed-loop filaments have also been noted in *Antennarius caudimaculatus* eggs by Pietsch and Grobecker (1980). Bar = 1,000 μm. (C) Chorion of *Paracallionymus costatus* collected off South Africa. The surface features are irregular and cover the entire egg surface. This differs from species of *Callionymus*, which have hexagonal patterns. Bar = 10 μm. (D) Chorion surface of *Mugil cephalus*. These structures are irregular and cover the entire egg surface. Note the superficial similarity to *Paracallionymus*. Bar = 10 μm. (E) Chorion surface of an advanced ovarian egg of *Coryphaenoides filifer*. Note that the surface "blebs" are arranged in hexagonal patterns and may be the precursors of a hexagonal pattern typical on eggs in this family. The pelagic egg of this species has not been described. Bar = 10 μm. (F) Chorion surface of an advanced ovarian egg of *Coryphaenoides acrolepis*. The hexagonal ridges are better developed than in Fig. 19E. There are holes under the ridges between the intersections, which might indicate that this species, whose egg is also undescribed, may have the hexagonal network supported on "stilts" as described for eggs of *Coelorhynchus* spp. (Robertson, 1981; Sanzo, 1933a). Bar = 10 μm.

Fig. 20. (A) Spines on the chorion surface of *Oxyporhamphus micropterus*. These are distributed over the entire surface of the egg. Bar = 100 μm. (B) Chorion surface from *Scomberesox saurus* collected off South Africa. The tufts are characterized by a relatively complex basal morphology and depending upon method of fixation, may resemble small bundles of hairs or, as here, simply coalesced tufts. Bar = 10 μm. (C) Micropyle and associated pores of the egg of *Lactoria diaphana* from the Eastern Tropical Pacific. The pores shown here are restricted to this region around the micropyle and appear to penetrate the outer layer of the chorion. Bar = 50 μm. (D) Secondary, smaller pit structures on the remainder of the egg of *Lactoria diaphana*. I refer to these depressions as "pits" because closer examination does not reveal penetration through any layer of the chorion, as opposed to the pores surrounding the micropyle in 20C. Bar = 1 μm. (E) Head region of a larval *Sebastes melanops* shortly after parturition. Polygonal epidermal cells may be noted on some parts of the body. Bar = 100 μm. (F) Epidermis on the dorsal surface, just posterior to the head, on an embryonic *S. melanops* approximately 28 days post fertilization. Note the distinct microridges and cell borders characteristic of developing teleost epidermis. Bar = 10 μm.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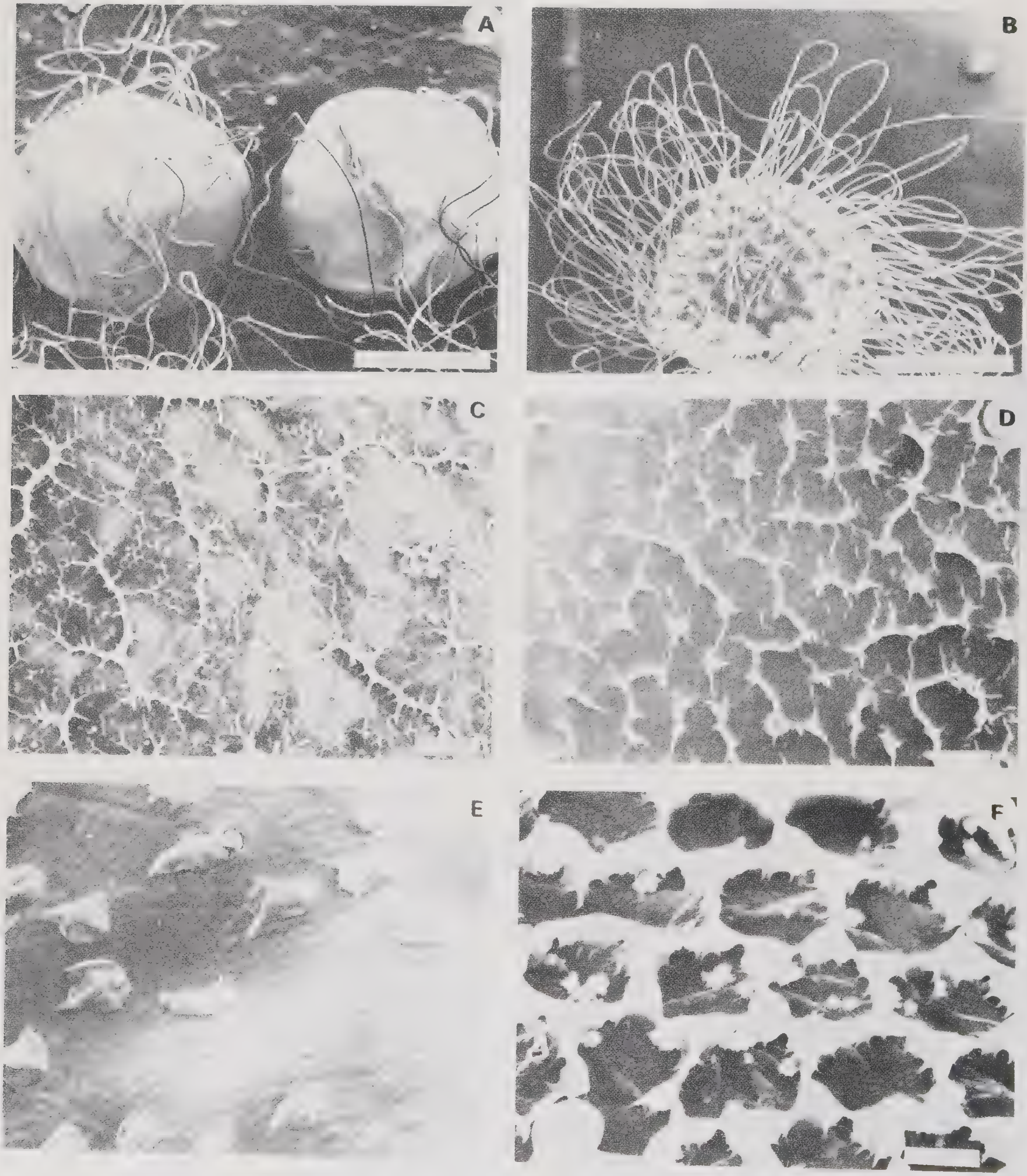
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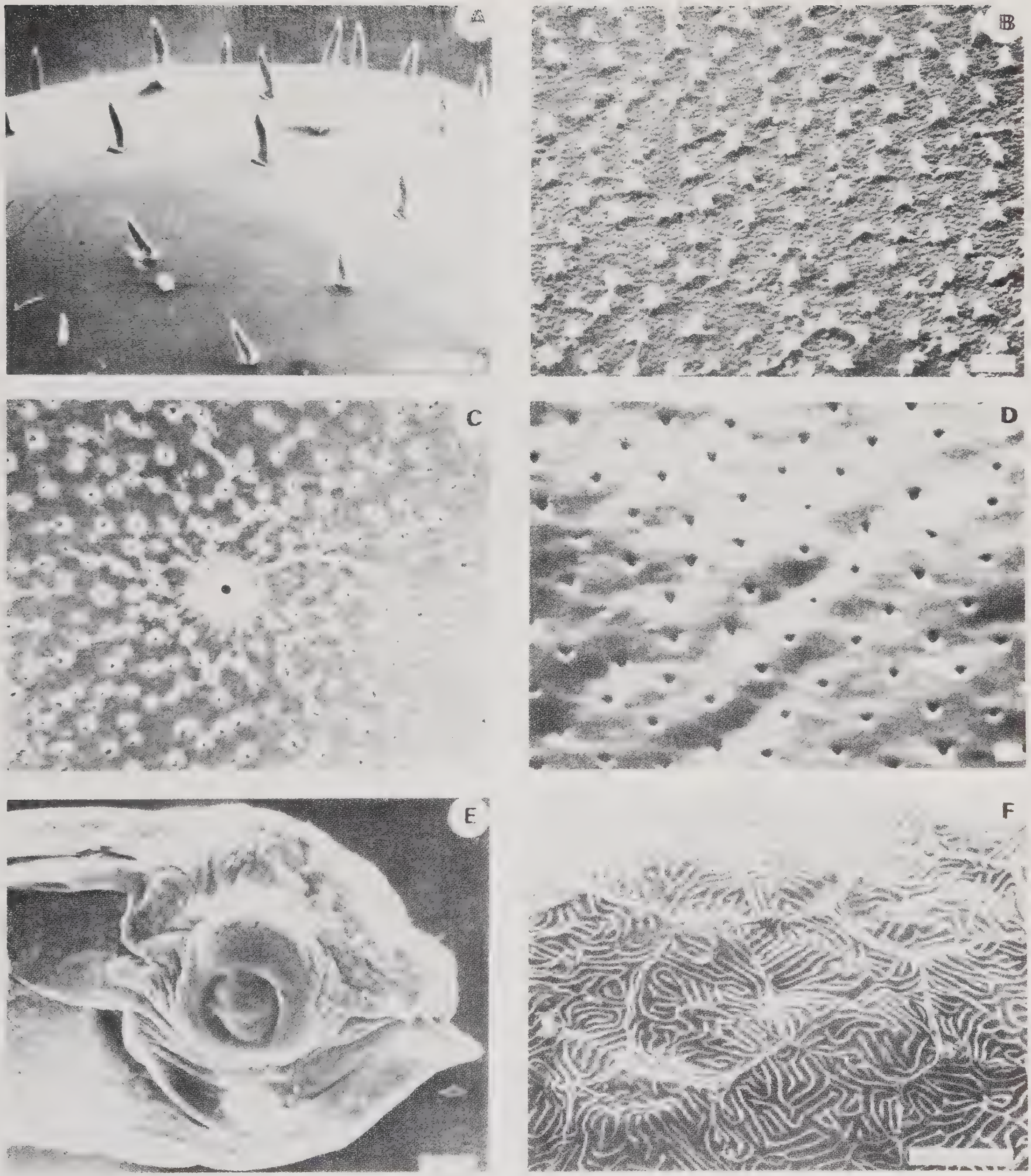
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(Fig. 18C) as compared to that of *Pleuronichthys coenosus* (Fig. 18E, F). Here, the hexagons are not only smaller, but the area within the facets does not appear porous. SEM was used for this species and its congeners for egg description by Sumida et al. (1979). It is interesting to note that these authors discussed the similarity in chorion structure of *Pleuronichthys* spp. with that of *Synodus lucioceps.* While there were slight differences in sizes of the polygons, the superficial similarity of chorion structure on these phylogenetically distant genera supports a functional role (Robertson, 1981) and independent derivation. In this instance, however, SEM was valuable for understanding and interpreting the differences between species and genera subsequently observed under the light microscope (Sumida et al., 1979). Similarly, Keevin et al. (1980) used chorion ornamentation to distinguish among genera of killifishes.

Other ornamentations include more random ridges (*Paracallionymus costatus,* Fig. 19C, and *Mugil cephalus,* Fig. 19D), filaments of varied length, diameter, and base morphology (*Atherinopsis californiensis* and *Atherinops affinis,* Fig. 19A, B; see also Hubbs and Kampa, 1946), tufts (*Scomberesox saurus,* Fig. 20B), spines (*Oxyporhamphus micropterus,* Fig. 20A), and pits and pores (*Lactoria diaphana,* Fig. 20C, D). In the callionymids, the small eggs of species of *Callionymus* have hexagonal sculpturing similar to that of *Pleuronichthys* (Fig. 18E). In *Paracallionymus costatus* (Fig. 19C), however, random ridges similar to those in *Mugil cephalus* are apparent.

Since chorion microstructure is formed by follicle cells during oogenesis (Sponaugle and Wourms, 1979; Stehr, 1979), patterns may also be discerned in ovarian eggs. The pelagic eggs of macrourids are poorly known but have been described for selected species by Sanzo (1933a), Robertson (1981), and Grigor'ev and Serebryakov (1981). For Pacific species of *Coryphaenoides,* pelagic eggs remain poorly known but apparently have hexagonal patterns as in other members of the genus; this is clearly shown in ovarian eggs near the maximum size observed by Stein and Pearcy (1982; Fig. 19E, F). Thus SEM of developing ovarian eggs may be used to discern differences which then aid in identification of eggs from plankton samples.

For larval stages, SEM has been used for the description of development of several surface structures, such as the olfactory organ (Elston et al., 1981) and lateral line neuromasts (Dobbs, 1974). For taxonomic studies, differentiation of fine-scale morphological differences, such as dentition or fine-scale spine serration, may be useful. Its most valuable use may therefore be for later larval development, since pigmentation and other characteristics in early larvae are better seen with conventional methods (Fig. 20E, F).

To conclude, SEM may serve as an adjuct to traditional methods in the description of fine structure in fish eggs and larvae. For high magnification, high resolution visualization of surface morphology, it remains the most effective tool available. Under lower magnifications, it may allow one to clearly visualize structures which are difficult to interpret using standard microscopical methods (Fig. 18A, B).

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CARBON ASSIMILATION AS A FUNCTION OF INGESTION RATE IN LARVAL PACIFIC HERRING, *CLUPEA HARENGUS PALLASI* Valenciennes

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Abstract: During the larval stage, clupeoids and other fishes are characterized by straight, relatively undifferentiated guts. Where it has been studied in detail, the evacuation rate in these larvae appears to be directly related to ingestion rate, which is in turn related to food concentration. Qualitative assessments have suggested that the degree of digestion of food particles is inversely related to the rate of evacuation. In the present study, early larvae of the Pacific herring, *Clupea harengus pallasi* Valenciennes, were fed for 1 h upon ^{14}C-labelled rotifers, *Brachionus plicatilis* Muller, and *Artemia* nauplii at high densities. At the end of 1 h, larvae were transferred to six food densities, ranging from 0 to 10 unlabelled prey $\cdot$ ml^{-1}. After 22 h, larvae were removed from the feeding tanks and sacrificed. The labelled carbon remaining in the larvae as a function of the percent consumed after the 1-h feeding interval was used as an index of carbon assimilation. The percent carbon retained decreased significantly with increasing food concentration. Larval herring thus decrease carbon assimilation from individual food particles at high food densities. The magnitude of increasing ingestion, however, more than compensates for the decreased carbon assimilation, and larvae gain greater total energy under conditions of high food concentration. The results support the suggestion that clupeoid larvae are adapted to utilize high food concentrations associated with plankton patches in the pelagic environment.

Introduction

Survival of larval fishes is dependent upon adequate food resources. In early larvae, high mortality resulting from low food densities may result in critical periods which can ultimately affect year class strength (Hjort, 1914). More recent work demonstrates that the food must be of the appropriate type (Scura & Jerde, 1977) and must also be distributed on the appropriate scale (Lasker, 1975; Lasker & Zweifel, 1978). The scale of distribution results in varying concentrations of prey, which are apparently utilized differently by larvae of different fish taxa. Larvae of the clupeoid *Engraulis mordax* require food densities greatly in excess of average densities found in the sea (O'Connell & Raymond, 1970). Lasker (1975) later showed that sufficient food densities existed in specific patches in the sea, and Hunter & Thomas (1974) demonstrated that larvae alter search behavior to increase the probability of remaining in those patches once found.

The work of Houde (1978), and Houde & Schekter (1981, 1983) suggests that the above pattern does not characterize all larval fishes. They compared the survival, growth, and energetics of larval clupeiform, pleuronectiform, and perciform fishes and demonstrated striking differences. For all three taxa, the ration consumed depended on

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food density; the clupeiform could consume the highest ration at high food density, but it had the lowest growth efficiency (Houde & Schekter, 1981, 1983). Furthermore, to achieve the same growth and survival as the other taxa, 2–10 times the food density was necessary for the clupeiform, *Anchoa mitchilli* (Houde, 1978).

The above observations on clupeiform larvae support the contention of Griffiths (1975) that larval fish are number maximizers, consuming prey at nearly the rate they are encountered, as opposed to energy maximizers, which forage and process prey to maximize net energy. Other work supports this idea. Werner & Blaxter (1980), working with larval *Clupea harengus*, noted marked increases in evacuation rate with increasing prey concentration. Visual observations showed that digestion was poor at high prey densities, and they suggested that assimilation may decrease with increasing prey density. Similarly, Chitty (1981) noted food residence times as low as 7 min in the gut of larvae of the clupeoids *Anchoa mitchilli* and *A. lamprotaenia*. Thus, as prey density varies, the energy extracted from individual prey may change. The magnitude of this change in assimilation, however, is unknown. If low enough, additional prey may result in little net gain in energy with increasing ration. In other continuous feeders, this has been termed superfluous feeding (Beklemishev, 1962). In the present study we estimate an index of carbon assimilation and total carbon intake in larvae of the Pacific herring, *Clupea harengus pallasi* Valenciennes, as a function of prey concentration.

Materials and Methods

Herring larvae were laboratory-reared from eggs which had been spawned naturally on inter- and subtidal algae in Yaquina Bay, Oregon on 15 April 1982. Culturing and all experiments were conducted in a temperature and light-controlled room (10 °C; 9 h light : 15 h dark) in filtered sea water at 15‰ salinity. After hatching, larvae were maintained on the rotifer, *Brachionus plicatilis*, cultured after the methods of Theilacker & McMaster (1971).

B. plicatilis and the naupliar stage of *Artemia salina*, both common food organisms used in larval fish rearing, were labelled with ^{14}C following methodology of Sorokin (1966) and Govoni *et. al.* (1982). The unicellular marine alga, *Isochrysis* sp. (Ewart & Epifanio, 1981), was cultured for 1 wk at 18 °C and pH 8.8 in 2.8 l of media with 200 μCi ^{14}C sodium bicarbonate (New England Nuclear). *Brachionus* were innoculated into a labelled algal culture at 16 rotifers $\cdot$ ml^{-1} and allowed to incorporate the isotope for 1 wk; newly-hatched *Artemia* nauplii were fed labelled algal culture for 48 h at 54 nauplii $\cdot$ ml^{-1}. Labelled food organisms were acclimated overnight to 10 °C and allowed to evacuate guts of labelled algae prior to feeding them to the larval herring.

On Day 16 post hatching, ≈300 herring larvae, with mean notochord length (NL) of 10.3 mm, were transferred to a 10-l black plastic pot and held in darkness for 15 h without food, which allowed complete gut evacuation. In the morning, larvae were fed with labelled *Brachionus* at 30 rotifers $\cdot$ ml^{-1}. Six larvae were removed from the feeding tank at each of the following intervals: 0, 0.25, 0.5, 0.75, 1, and 2 h after initial feeding to establish a time–ration relationship. At each time, these larvae were divided into two replicates of three larvae each, which were prepared for liquid scintillation counting (LSC). After 1 h of feeding on labelled prey, other groups of larvae were transferred to 10-l tanks containing non-labelled *Brachionus* at concentrations of 0, 0.2, 0.5, 1.0, 5.0, and 10.0 rotifers · ml^{-1}. Great care was taken during transfers to ensure that only larvae, and no labelled food, were transferred. At 22 h after larvae were removed from labelled food, when intestines in all feeding groups were free of labelled food, three replicates of five larvae from each concentration were prepared for LSC.

Similar feeding experiments were conducted using the larger food organism, *Artemia* nauplii. At 31 days post hatching, herring larvae (mean NL of 13.8 mm) were starved as above prior to being fed with ^{14}C-labelled *Artemia* at 15 nauplii · ml^{-1}. Larvae were taken from the feeding tank on the same schedule as above, but with three replicates of two larvae each prepared for LSC. Again, larvae were transferred to tanks containing non-labelled food 1 h after feeding began. The densities for the *Artemia* experiments were 0, 0.03, 0.3, 1.5, 3, and 10 nauplii · ml^{-1}. Three replicates of four larvae per food density were prepared for LSC 22 h after being transferred from the labelled food tanks. Again, all labelled food was evacuated from the larval guts.

Larval herring sampled for LSC were removed from the experimental tanks with a large-bore pipette, placed into a watch glass, and handled with forceps to avoid contamination with labelled food. Larvae were digested in scintillation vials with 1 ml of tissue solubilizer (Beckman BTS) for 24 h at 55 °C, cooled to room temperature, and counted in 10 ml of Ready-Solv EP fluor (Beckman). Chemiluminescence was reduced by the addition of 0.1 ml glacial acetic acid to each sample and by dark adapting samples prior to counting. Both labelled food organisms were analyzed for activity prior to feeding experiments. An aliquot of 10 ml was removed from each of the two labelled cultures; food organisms were enumerated and filtered onto tared glass fiber filters. After drying overnight at 55 °C, the filters were weighed to the nearest μg and solubilized and counted as previously described. Counts per minute (CPM) were corrected for counting efficiency by developing a quench curve with standard, calibrated samples of ^{14}C prepared in a manner similar to experimental samples, and were expressed as disintegrations per minute (DPM).

To account for respired ^{14}C and that defecated as particulate organic ^{14}C, after 1 h feeding on labelled *Artemia*, three larvae were placed in each of four Gilson respirometer flasks with 0.5 ml of 10% KOH in the center well with filter paper as a trap for carbon dioxide; larvae were held in 8.0 ml of sea water. After removal of larvae with forceps, the liquid in the vessel was acidified with 0.5 ml of concentrated sulfuric acid, immediately sealed, and held for 2 h while carbon dioxide was adsorbed onto the filter paper. Samples prepared for LSC from each of the four replicates included (1) the filter paper with KOH, (2) three larvae solubilized as above, (3) particulate carbon collected on 0.3-μm glass fiber filters and solubilized, (4) a blank filter with filtrate passed through, and (5) 1 ml of filtrate to assay for dissolved organic ^{14}C.

For describing relationships between variables, logarithmic and exponential functions were fit to data. Where percentages were used, values were arcsin transformed prior to analysis.

RESULTS

Larval herring readily fed during the experiments on both labelled and unlabelled *Brachionus plicatilis* and *Artemia salina* nauplii. Because larval herring are continuous feeders in daylight, the food uptake curves should be approximately asymptotic; for our experiments it was important to choose a time slightly before the gut was completely full to prevent defecation of ^{14}C labelled prey. For both *Brachionus* and *Artemia*, uptake of ^{14}C as a function of time was characterized by asymptotic curves (Fig. 1). The curves are described by the following relationships:

$$\textit{Brachionus}\text{: } (\text{DPM} \cdot \text{larva}^{-1}) = 1059.7[\ln(t+1)] - 401.8$$
$$n = 12,\ r^2 = 0.68\ \ (P < 0.01)$$
$$\textit{Artemia}\text{: } (\text{DPM} \cdot \text{larva}^{-1}) = 532.6[\ln(t+1)] + 356.5$$
$$n = 18,\ r^2 = 0.31\ \ (P < 0.025)$$

These relationships predict ^{14}C consumed at 60 min to be 3955 DPM · larva^{-1} for *Brachionus* and 2546 DPM · larva^{-1} for *Artemia*. Given the mean value of ^{14}C in *Brachionus* (89.3 DPM) and *Artemia* (684.9 DPM), this suggests that mean consumption was 44.3 *Brachionus* and 3.7 *Artemia* during the 1-h period of feeding on labelled food. These are reasonable estimates of feeding rates at these densities for larvae near this age (Werner & Blaxter, 1980).

In all feeding experiments, the 22-h period after exposure to ^{14}C-labelled food was sufficient to result in complete evacuation of labelled particles, even at the zero food level, as shown by microscopic observations. Where larvae were fed labelled *Brachionus*, the amount of carbon retained (in DPM · larva^{-1}) decreased significantly with increasing food density (Table I; Fig. 2). Expressed as a percentage of the ingested ^{14}C

TABLE I

Results from feeding experiments with *Brachionus plicatilis*: the caloric content of *Brachionus* was calculated from the mean value in Theilacker & Kimbrell (1984); each of the three replicates was based upon the mean of five larvae; the value represents the ^{14}C retained after 22 h.

Food density (*Brachionus* · ml^{-1})	cal · l^{-1}	*N*	Mean DPM · larva^{-1}	SE
0	0	3	1892	242
0.2	0.26	3	1734	125
0.5	0.66	3	2032	313
1.0	1.32	3	1807	40
5.0	6.60	3	1346	19
10.0	13.20	3	1523	119

(calculated from the relationship in Fig. 1A) and arcsin transformed, the relationship is expressed as follows:

$$\arcsin (C) = 43.467 \exp[-0.074 \ln (f + 1)]$$
$$n = 18, \ r^2 = 0.313 \ (P < 0.025)$$

where C = percent ingested carbon and f = food density (*Brachionus* $\cdot$ ml^{-1}).

Similar results were observed with herring larvae fed *Artemia* nauplii. Again, ^{14}C retained (DPM $\cdot$ larva^{-1}) decreased from very high values in the experiment with no

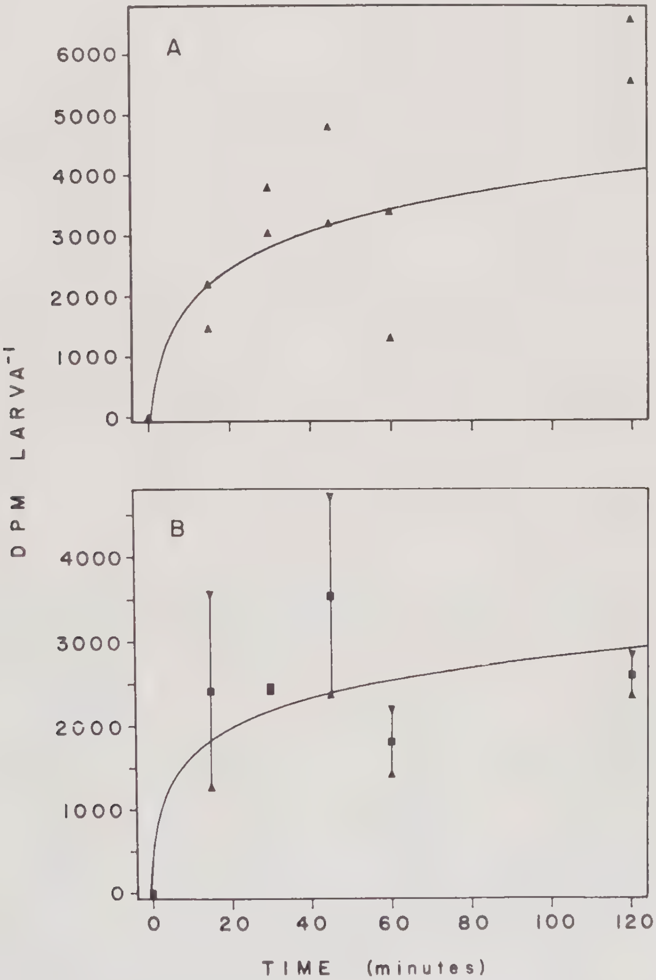

Fig. 1. Uptake of ^{14}C by larval *Clupea harengus pallasi* as a function of time: A, 4-wk-old larvae feeding on *Brachionus*, the points represent the two replicates at each time; B, 6-wk-old larvae feeding on *Artemia* nauplii, points shown are the means of three replicates ± 1 SE; in both cases, the fitted curve is described in the text.

food (Table II; Fig. 3). The range of predicted values of carbon retained was generally greater for *Artemia* than for *Brachionus*. This may be due to the fact that the protocol for labelling *Brachionus* with ^{14}C required 7 days and population growth, whereas that for *Artemia* took only 30 h; thus significant proportions of the ^{14}C in *Brachionus* may have been in indigestible lorica. Indeed, in similarly labelled *Brachionus*, Govoni (1980) noted 66% of the ^{14}C in protein, 7% in lipids, 4% in carbohydrates, and the remainder in unextracted, and probably undigestible, components. An alternative explanation is related to size and foraging costs. Individual *Brachionus* are smaller and contain only

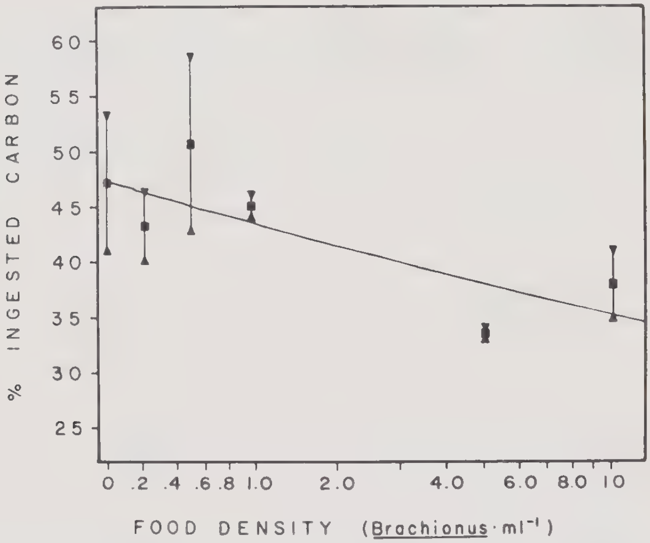

Fig. 2. The percentage of ingested ^{14}C retained per herring larva after 22 h feeding on non-labelled *Brachionus*: the data are fit with an exponential curve described in the text; data points are means of three replicates ± 1 SE.

TABLE II

Results from feeding experiments with *Artemia salina* nauplii: the caloric content of *Artemia* was calculated from the value of 0.00937 cal · nauplius^{-1} in Benijts *et al.* (1975); each of the three replicates was based upon the mean of four larvae; the value represents the ^{14}C retained after 22 h.

Food density (*Artemia* · l^{-1})	cal · l^{-1}	*N*	Mean DPM · larva^{-1}	SE
0	0	3	2091	302
0.03	0.28	3	1179	228
0.30	2.81	3	1209	172
1.50	14.06	3	736	128
3.00	28.11	3	1066	83
10.00	93.70	3	956	183

14% the calories of *Artemia*; thus, foraging costs to obtain a given ration are higher and the respiratory utilization of ^{14}C during the 22-h period may be higher. Expressed as a percentage of the ingested ^{14}C (calculated from the relationship in Fig. 1) and arcsin transformed, the relationship is as follows:

$$\arcsin (C) = 47.80 \exp[-0.144 \ln (f + 1)]$$
$$n = 18, r^2 = 0.208 \ (P < 0.05)$$

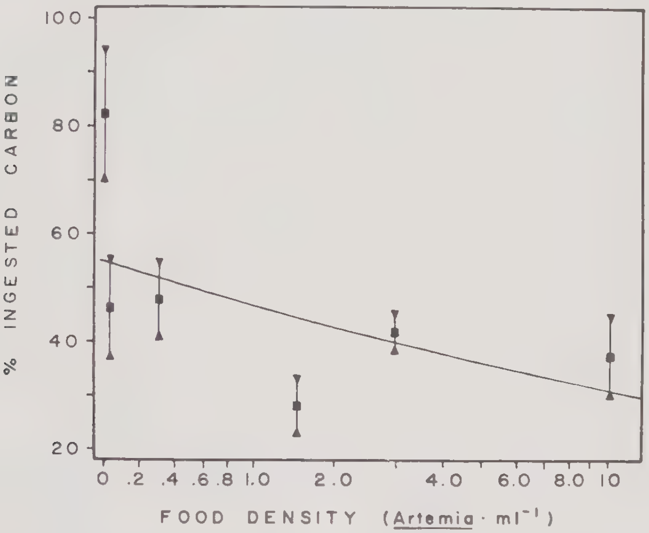

Fig. 3. The percentage of ingested ^{14}C retained per herring larva after 22 h feeding in non-labelled *Artemia* nauplii: the data are fit with an exponential curve described in the text; data points are means of three replicates ± 1 SE.

The percent carbon retained may only be considered as an index of assimilation (Govoni *et al.*, 1982), since short-term carbon pools may be recycled or used as respiratory substrates (Conover & Francis, 1973). The experiments with ^{14}C *Artemia* fed larvae in retention chambers were conducted to estimate the carbon retained, respired, and defecated (Table III). The dissolved ^{14}C remaining after acidifying the filtrate represented an average of 8.2% of the total ^{14}C in the retention chambers. The particulate carbon from the retention chambers may be considered as non-assimilated feces; thus our estimate of assimilation is 58.5% at zero food density with *Artemia*. Of this amount, 19.5% is respired during the 22-h interval between feeding with labelled food and sacrifice. This value allows us to adjust the carbon retained after 22 h to a closer index of carbon assimilation for experiments with *Artemia*.

Discussion

Two other studies have been conducted on energetics of larval fishes using ^{14}C as a tracer to follow carbon uptake and assimilation after the general techniques of Sorokin (1966); both studies, however, have considered percoid larvae. Sorokin & Panov (1966) studied the energetics of the larvae of the freshwater fish *Abramis brama* and noted assimilation values of ≈75–80% of ingested carbon. Govoni *et al.* (1982), using a larval sciaenid (*Leiostomus xanthurus*), observed a mean carbon absorption of 87.6%. While neither of these studies estimated the effect of varying food density, they observed no change in assimilation with increasing larval age. In our study, the estimate of carbon assimilation depends upon food density. The estimates for herring larvae feeding on *Artemia* from Fig. 3, corrected for respiration (Table III), decrease exponentially from 68.2% at 0.001 *Artemia* $\cdot$ ml^{-1} to 38.5% at 10.0 *Artemia* $\cdot$ ml^{-1}. Assuming the same respiratory fraction for larvae feeding on *Brachionus*, corrected estimates from Fig. 2 are 58.8% at 0.001 *Brachionus* $\cdot$ ml^{-1} to 43.7% at 10 *Brachionus* $\cdot$ ml^{-1}. The high values in Govoni *et al.* (1982) may have resulted from using retention chambers free from food, resulting in maximum assimilation under non-steady state feeding conditions. Our lower estimate of assimilation may relate to the type of larva; clupeoid larvae, such as *Clupea harengus*, have straight guts with no intortion (O'Connell 1981). Houde & Schekter (1981, 1983) observed the lowest growth efficiency in clupeiform larvae among larvae from three orders. Thus our estimates of carbon assimilation are near expected levels.

The decrease noted in assimilation efficiency (Figs. 2,3) correlates well with past qualitative observations on clupeoid larvae, particularly those of Werner & Blaxter (1980). They noted decreasing evacuation times with increasing prey density for *Clupea harengus* larvae feeding on *Artemia* nauplii. Similarly, Laurence (1971) noted nearly a doubling of evacuation time when larvae with a full gut were deprived of food as compared to those which were fed. Larval herring and many other fish larvae are continuous feeders in daylight; other continuously feeding animals show similar responses. Doohan (1973) noted that when food was in excess, assimilation efficiency in the rotifer *Brachionus plicatilis* decreased markedly; this effect was due to particles passing through the gut so rapidly that they were not effectively digested. Similarly, Reeve *et al.* (1978) observed decreasing assimilation with increasing food density in a ctenophore. Cushing (1959) suggested that copepods may consume 5–10 times more food than they need. This phenomenon has been described as "superfluous feeding" (Beklemishev, 1962), defined as when continuously feeding animals do not increase assimilation in response to an increase in standing stock of their food. Conover (1966), however, observed no decrease in assimilation with increasing ingestion and stated that superfluous feeding "does not normally occur in nature". For fish larvae, however, it should be pointed out that feeding does not occur in the dark; thus the effects of any superfluous feeding would not be as great as in a true continuous feeder.

The important question about the reduced assimilation efficiency is its interaction with feeding rate. Werner & Blaxter (1980) observed defecation of live *Artemia* nauplii from the guts of larval *Clupea harengus* at the highest food densities tested. If the decrease in assimilation efficiency is not counteracted by a greatly increased feeding rate, then total carbon assimilated may decrease, a situation similar to that of superfluous feeding (Beklemishev, 1962). Werner & Blaxter (1981) described the feeding rates of larval *Clupea harengus* as a function of age. As a function of food density (in calories $\cdot l^{-1}$), the data for 6-wk-old larvae fit a model of exponential increase as follows:

$$\text{cal} \cdot \text{h}^{-1} = 0.0392 \exp[0.2915 \ln (\text{cal} \cdot \text{l}^{-1})]$$
$$n = 5, \; r^2 = 0.932 \; (P < 0.001)$$

This relationship predicts increasing consumption from 0.005 cal $\cdot$ h^{-1} at a food level of 0.001 cal $\cdot$ l^{-1} to 0.150 cal $\cdot$ h^{-1} at 100.0 cal $\cdot$ l^{-1} (Fig. 4). The relationship between *Artemia* density and the percent carbon retained (Fig. 3) was recalculated after changing *Artemia* density to cal $\cdot$ l^{-1} (after Benijts *et al.*, 1975) and correcting the percent ingested

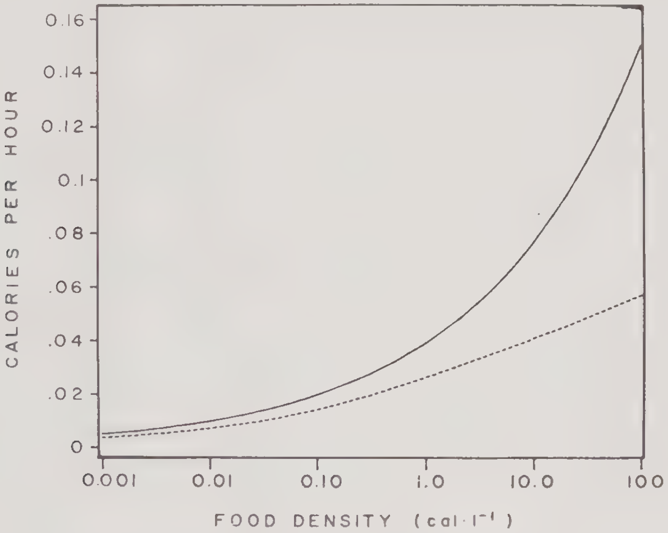

Fig. 4. The relationship of calories consumed (———) and calories assimilated (------) as a function of food density for 6-wk-old larval *Clupea harengus* feeding on *Artemia* nauplii: the solid line is based on the equation given in the text calculated from Werner & Blaxter (1981); the dashed line is the product of this relationship with assimilation calculated from the present study.

TABLE III

Distribution of labelled carbon after 22 h in an isolation flask: each flask contained three larvae; the particulate fraction (retained on a 0.3-μm glass fiber filter) represents the feces; CO_2 represents respiration by larvae over the 22 h; carbon assimilation is therefore represented by the sum of (larva + CO_2).

Source	*N*	Mean % of total	SE
Larva	4	47.1	4.4
CO_2	4	11.4	0.6
Particulate	4	41.5	5.0

carbon to assimilation efficiency based upon respiration (Table III). The resulting relationship,

$$\arcsin(\text{assimilation}) = 58.64 \exp[-0.0953 \ln(\text{cal} \cdot \text{l}^{-1} + 1)]$$
$$n = 18,\ r^2 = 0.334\ (P < 0.01)$$

when multiplied by feeding rate, gives the calories assimilated per hour as a function of food density (lower curve, Fig. 4). The results suggest that total assimilation continues to increase despite a decreasing assimilation efficiency. When taken together, these curves would suggest that although growth may continue to increase, gross growth efficiency should decrease at high food concentrations and ingestion rate. Checkley (1982) observed increasing gross growth efficiency with increasing ingestion rate in *Clupea harengus* larvae, but suggested that gross growth efficiencies would decrease at higher ingestion rates. This is similar to gross growth efficiencies in juvenile and adult fishes, which typically decrease above some optimum ration (Brett & Groves, 1979; Boehlert & Yoklavich, 1983). Our data therefore support a departure from Blackman kinetics, where ingestion alone limits growth (Condrey, 1982).

Larval fishes depend upon patchiness of both conspecifics (Hewitt, 1981) and of prey (Hunter, 1981) to different degrees. Lasker (1975, 1978) demonstrated that first-feeding larvae of *Engraulis mordax* depend upon a stable ocean for development of the patches with appropriately sized food particles at densities of 20–40 $\cdot$ ml^{-1}. These high densities are necessary for survival (O'Connell & Raymond, 1970; Hunter, 1972; Lasker & Zweifel, 1978). Larval stages of clupeoids, such as anchovies and herrings, are apparently able to exploit these patches by continually increasing ingestion rate. Energetic analysis suggests a decrease in assimilation and gross growth efficiency (Houde & Schekter, 1980, 1981, 1983; present study); thus, as other continuous feeders, these clupeoid larvae fit the characterization of number maximizers (Griffiths, 1975). Within the constraints of uniformly sized prey in our experimental system, *Clupea harengus* larvae also maximize energy through maximizing numbers.

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REPRODUCTION, EMBRYONIC ENERGETICS, AND THE MATERNAL-FETAL RELATIONSHIP IN THE VIVIPAROUS GENUS *SEBASTES* (PISCES: SCORPAENIDAE)

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ABSTRACT

Reproduction in the scorpaenid genus *Sebastes* has been characterized as primitive ovoviviparity. In the black rockfish, *S. melanops,* egg size is small (0.8 mm), but the gestation period is 37 days and larvae at birth are well developed, with a remnant of yolk and the ability to initiate feeding. To test the hypothesis that this species is viviparous with additional maternal nutrition, we studied embryonic energetics and morphology. Catabolism during development utilized 64% of the yolk energy, resulting in a maximum yolk utilization efficiency of 36%, similar to oviparous fishes. Calorimetry, however, demonstrates that 81% of the initial yolk energy is present at birth. Thus approximately 70% of the catabolic energy is contributed by the maternal system during gestation. Microscopic analysis of embryonic epidermis suggests no specializations for nutrient uptake. Histological observations, however, reveal that the hindgut is functional approximately 22–25 days after fertilization. Thus, we suggest that nutrition occurs through consumption and assimilation of ovarian fluid.

Reproductive modes in the Scorpaenidae have apparently evolved from simple oviparity in seven of eight subfamilies, to lecithotrophic viviparity in more primitive members of the subfamily Sebastinae, through matrotrophic viviparity in *Sebastes.* This pattern involved progressively longer retention of embryos until after organogenesis and functional differentiation of the gut, facilitating this rather primitive form of embryonic nutrition among matrotrophic viviparous species.

INTRODUCTION

Reproductive modes in the teleost fishes historically have been grouped into the categories oviparity, ovoviviparity, and viviparity. Oviparous species shed gametes from the body and fertilization and embryonic development are external. In ovoviviparity and viviparity [referred to herein as lecithotrophic and matrotrophic viviparity, respectively, after Wourms (1981)], fertilization is internal and development proceeds within the female reproductive system. The evolution of these reproductive modes involved a compromise between high reproductive rates with low survival and low reproductive rates with high survival. The former is exemplified in the oviparous fishes, the latter in viviparous fishes, although variations exist within each mode of reproduction. The traditional differences between lecithotrophic and matrotrophic viviparity involve the provision of maternal nutrition after oogenesis; it is lacking in strictly lecithotrophic viviparous species. There is a continuum of levels of maternal nutrition in matrotrophic viviparous fishes, but in most species the actual maternal-fetal relationships during gestation are unknown (Wourms, 1981). The coelacanth

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Latimeria, for example, was described as a lecithotrophic viviparous species by Smith *et al.* (1975), but was later shown to be a matrotrophe despite a lack of specialized structures for nutrient uptake (Wourms *et al.,* 1980). Further research on the maternal-fetal relationship will help us understand the evolution of viviparity in fishes (Wourms, 1981).

In the family Scorpaenidae, live-bearing is present in the subfamily Sebastinae. The most advanced genus, *Sebastes,* has a center of distribution in the North Pacific and is comprised of some 106 species worldwide (Barsukov, 1981). Reproduction in this genus is considered to be primitive among viviparous species, with no maternal nutrition (Wourms and Cohen, 1975; Wourms, 1981). Fecundity approaches that of the most highly fecund oviparous species, with individual fecundity to 2,300,000 in *S. paucispinis* (Phillips, 1964) and weight specific fecundity reaching 500 eggs per gram body weight (MacGregor, 1970; Boehlert *et al.,* 1982). Egg sizes range from about 0.7 to 1.5 mm, the gestation period is approximately 1–2 months long, and larval size at birth is relatively small, ranging from 4 to 9 mm (Fujita, 1957; Moser *et al.,* 1977). The larvae are relatively well developed, however, and are generally born at a developmental stage with organogenesis complete, jaws developed, and the ability to initiate feeding. Moser and Butler (1981), in an attempt to rear larvae of *S. dalli,* suggested that the lack of success in rearing *Sebastes* larvae may be related to the timing of birth; larvae in the wild are well developed at birth whereas those used in laboratory rearing are typically born prematurely. They speculated that additional maternal nutrition might be critical to complete organogenesis late in gestation. To test the hypothesis that reproduction in *Sebastes* is matrotrophic viviparity, we describe the energetics and nutrition of embryonic black rockfish, *S. melanops,* during gestation.

MATERIALS AND METHODS

Experimental animals

Sebastes melanops is a fairly shallow-living rockfish, generally inhabiting waters from 8 to 55 m (Barsukov, 1981); adults inhabit nearshore rocky reefs from Baja California to the Aleutian Islands (Hart, 1973). All females are mature at an age of 9 years and a length of about 43 cm off Oregon (McClure, 1982), and give birth predominantly during January through March (Laroche and Richardson, 1980). Larvae are pelagic, as is typical of *Sebastes* (Ahlstrom, 1961), and emigrate to nearshore, intertidal, and estuarine areas at ages from 4 to 6 months (Boehlert and Yoklavich, 1983).

Adult *S. melanops* were collected on 8–9 January 1982 by hook and line from a sport fishing vessel off Seal Rock, Oregon in 10–20 m of water. Excess swim bladder gas was removed with hypodermic needles. Fish were held in large circular tanks (1.2 m diameter, 700-liter capacity) supplied with circulating sea water at 10°C (±1°C) during experiments. Following a 2-week period of adjustment to laboratory conditions, sex and stage of ovarian development were determined by catheterization and gentle suction; fish were tagged and segregated on the basis of reproductive state. Of the 16 females, 8 were gravid with embryos at various stages of development, 3 were preovulatory, and 5 were either immature or spent. The females with developing embryos were individually isolated in small circular tanks (0.7 m diameter, 120-liter capacity). Over time, despite separation from males, the three preovulatory females ovulated. The ova were fertilized, and subsequently underwent embryonic development. This is evidence of sperm storage since, in many species of *Sebastes,* insemination occurs up to six months prior to fertilization (Sorokin, 1961; Moser, 1967a).

Developing embryos were obtained by extracting ovarian samples from the 11 ripe females on a weekly basis from 22 January 1982 until parturition. Adult fish were anesthetized with tricaine methanesulfonate (MS-222; 75 mg/liter sea water) and catheterized using a sterile glass pipette. Oppenheimer's (1937) classification of developmental stages of *Fundulus heteroclitus* and Moser's (1967a) description of *S. paucispinis* development were used to identify stages of *S. melanops* embryos. Following Moser (1967a) and Shimizu and Yamada (1980), Oppenheimer's (1937) stages through stage 32 were found adequate for description of *Sebastes* development. Samples from different females from unfertilized eggs to extruded larvae, were taken for estimates of dry weight, ash, carbon and nitrogen, and for measurements of oxygen consumption. Examination of egg diameter from six different females revealed little variation, with mean 0.83 mm (standard deviation 0.026) and range 0.80–0.87 mm.

Calorimetry, nitrogen, and protein analysis

The maternal nutritional contribution to embryonic development was analyzed using bioenergetics and nitrogen and protein budgets. Calorimetry was used to estimate the energy content of developing embryos at eight stages, from unfertilized eggs to extruded larvae. After catheterization of gestating embryos, dry weights were measured to the nearest μg on a Perkin-Elmer AD-2Z microbalance. Groups of embryos were dried to a constant weight at 60°C. Ash content was determined after 3 hours combustion in a muffle furnace at 500°C. Samples were analyzed for carbon and nitrogen content using a Perkin-Elmer model 240-B carbon-hydrogen-nitrogen analyzer. The nitrogen-corrected equation from Salonen *et al.* (1976) was used to convert percent carbon to calories as follows:

$$\text{cal/embryo} = ([0.65\ (\%\text{C}) - 12.237]239)\ \text{W}$$

where C is carbon content per ash-free dry weight (AFDW) of sample and W is the AFDW of the embryo. While this method is based upon invertebrates, the estimated energy content of unfertilized yolk (6281 cal/g AFDW) is within the ranges of caloric estimates for marine fish eggs as summarized by Robertson (1974). Further, this relationship appears to hold for a diverse group of taxa, including phytoplankton and marine and freshwater protozoa (Finlay and Uhlig, 1981).

From additional specimens collected in 1984, protein content was determined for four developmental stages using the microbiuret method of Itzhaki and Gill (1964). Bovine serum albumin was used as a protein standard. The same specimens were analyzed for CHN content for comparison with 1982 specimens and to determine the percentage of protein nitrogen. This latter value was determined by dividing protein by 6.25.

Oxygen consumption

We measured respiration rates to compare the energy content of the developing embryos with the catabolic energy required during gestation. Embryos were removed by catheterization and placed in physiological saline (Forster and Hong, 1958) isosmotic with ovarian fluid (*ca.* 325 mOsM/kg, determined in a Wescor vapor pressure osmometer) in 15 ml respiration flasks. Experiments were performed in darkness at 10°C in a Gilson differential respirometer following standard techniques (Umbreit *et al.*, 1972). Embryos in respirometers were allowed to equilibrate for 0.5–1 hour prior to initial readings; subsequent readings were taken every 1–2 hours for 5–10 hours. Most experiments were performed with three replicates. Numbers and dry weights of embryos per vessel were determined upon completion of experiments and results were expressed as μl O_2/embryo/h and μl O_2/mg AFDW/h.

One of the problems in determining the total embryonic oxygen consumption during gestation is that *Sebastes* is viviparous; it is therefore difficult to establish a zero time for fertilization. Length of time spent at each stage of development was determined from samples of embryos taken by successively catheterizing females during gestation, at approximately weekly intervals. By determining the change in stage over the interval, we were able to estimate the duration of each Oppenheimer stage at 10°C. Using these estimates, we integrated the time spent at all stages to calculate a gestation period and also to estimate the total oxygen consumption during the gestation period. We felt that this estimate would be based upon the maximum number of females and would minimize individual variability.

Morphology

Histology of the alimentary tract and the surface structure of the epidermis were examined to determine the site of energy uptake in the developing embryos. For histological examination, small groups of catheterized embryos were preserved in isosmotic buffered 2% glutaraldehyde. Embryos were imbedded in acrylic resin (LR White), sectioned at 2 μm, and stained in hematoxylin and methylene blue-basic fuchsin after Bennett *et al.* (1976). The epidermis was examined with an AMR 1000 scanning electron microscope after fixation and preparation following Dobbs' (1974) methodology.

RESULTS

Stage duration and length of gestation

Length of time spent at each stage of development was determined from samples of embryos which were taken at intervals throughout gestation. Twenty-two samples from 8 fish provided 11 estimates to establish the relation between stage duration (D), measured in days/stage, and stage (S), which presented the midpoint of development stage between two sample intervals:

$$D = 0.0452S^{1.090}, \qquad n = 11, \qquad r^2 = 0.89$$

This relationship was nearly linear, with stage duration increasing with increasing stage number (Fig. 1). From the model of stage duration, a cumulative age of the embryo (time since fertilization) was calculated for stages 1 to 32 and plotted as a function of Oppenheimer developmental stage (Fig. 1). From stage 32 (estimated from the model to be reached in 31.2 days) to parturition, an average of 5.8 days elapsed for the 11 females in the study. The average gestation period at 10°C is therefore estimated to be 37 days. This agrees closely with our estimates from gestation periods of three individual fish which ovulated and were fertilized in the laboratory ($n = 3$, $x = 36.3$ days, $S = 0.58$).

Oxygen consumption rates

Embryonic *S. melanops* representing seven stages of development from eight females were used to determine total oxygen consumed during gestation. Depending upon stage of development, between 24 and 229 embryos were placed in each 15 ml respirometer flask. Embryos were judged to be inactive in respirometer flasks, but we could not observe activity during shaking of the flasks. Oxygen consumption

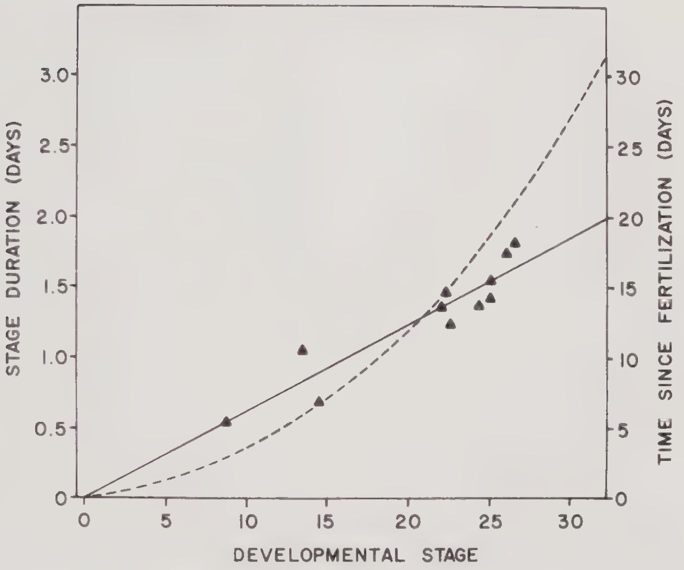

FIGURE 1. Duration of developmental stages during gestation of embryonic *Sebastes melanops* at 10°C. Developmental stages are determined according to Oppenheimer (1937). Stage durations (solid line) were estimated by successive catheterization of gestating females. The time since fertilization (dashed line) is an integration of the curve for stage duration; we estimate approximately 32 days to stage 32 and an additional 5 days until birth.

(μl/embryo/h) increased as embryonic development progressed (Fig. 2). The lowest oxygen uptake, averaging 0.0078 O_2/embryo/h, was measured from embryos in the earliest stage of development (stage 9 and approximately 2.4 days after fertilization as estimated from the stage duration model). The oldest embryos (stage 30 and 27.4 days after fertilization) utilized an average of 0.087 μl O_2/embryo/h. Oxygen consumption (Q, μl O_2/embryo/h), expressed as a function of time since fertilization (t, in days), is described by the equation:

$$Q = 0.00321t^{1.0026}, \qquad n = 8, \qquad r^2 = 0.98 \qquad \text{(Fig. 2).}$$

From this curve a cumulative estimate of oxygen required over the estimated gestation period of 37 days was determined to be 54.667 μl O_2/embryo. Using an oxycaloric equivalent of 0.005 cal/μl O_2 (Lasker, 1962), the catabolic component of energy used during gestation would correspond to 0.273 calorie.

Energy and protein changes during development

Measurements of weight and caloric content for developing embryos are presented in Table I. Eight stages are represented, including unfertilized eggs just prior to ovulation and the extruded larvae. In general, both weight and caloric content gradually decreased throughout development. The AFDW of an unfertilized egg was 67.5 μg. From the CHN analysis, percent carbon and nitrogen were determined and caloric content was estimated to be 0.429 calorie/egg. A correction was made for caloric contribution by the chorion to total available energy, since the chorion provides no energy to the embryo. The average chorion AFDW of 1.11 μg was converted to a caloric value of 0.005 calorie, assuming 50% carbon content. The available energy to the embryo is

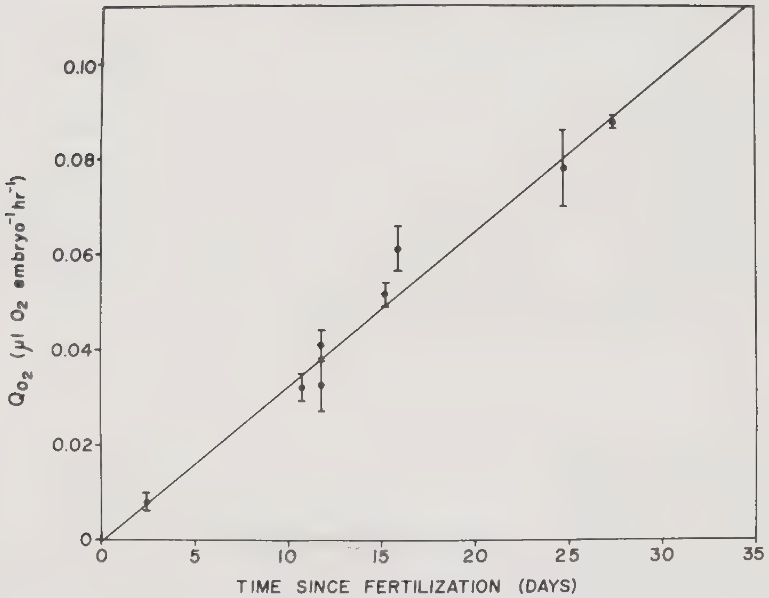

FIGURE 2. Oxygen consumption (µl O_2 embryo^{-1} h^{-1}) for embryonic *Sebastes melanops* as a function of time since fertilization at 10°C. Each point represents the mean of two to three observations on embryos from the same female; scale bars represent ±2 S.E.

therefore 0.424 calorie. At hatching, when the relatively well-developed larva still has a remnant of yolk, caloric measurements suggest that 81% of the initial egg energy remains in yolk and embryonic tissue. Nitrogen increases as a percentage of embryo dry weight with increasing time since fertilization, but this is balanced by decreasing total weight such that total nitrogen remains static (Table I; $n = 12$, $r = -0.23$, $P > 0.10$). Carbon, on the other hand, actually decreases with development (Table I; $n = 12$, $r = -0.92$, $P < 0.01$).

TABLE I

Weight, carbon, nitrogen, and caloric values of Sebastes melanops *embryos throughout gestation*

Oppenheimer stage	Dry weight embryo (µg)	AFDW embryo (µg)	Nitrogen (µg)	Carbon (µg)	C/N	Caloric content of embryo (cal/embryo)	Caloric content (embryo-chorion)
Nonfertilized egg	71	67.5	7.0	40.2	5.74	0.429	0.424
13	74	70.3	7.4	41.2	5.57	0.435	0.430
16	70	66.2	7.4	38.6	5.22	0.407	0.402
18	70	65.8	7.3	37.7	5.16	0.394	0.389
22	66	61.1	7.1	35.0	4.93	0.365	0.360
28	71	65.3	6.9	35.8	5.19	0.365	0.360
31	70	63.9	7.2	33.3	4.63	0.330	0.325
Larvae at birth	66.7	60.4	7.0	33.6	4.80	0.345	0.345

Developmental stages are determined after Oppenheimer (1937). (C/N = carbon to nitrogen ratio; AFDW = ash-free dry weight.)

If nonprotein nitrogen remained constant over development, total protein would remain static. In the 1984 examples, however, although the nitrogen remained static, protein decreased significantly during development ($n = 24$, $r = -0.73$, $P < 0.01$; Table II). These data suggest that nonprotein nitrogen increases from 1% in the earliest embryos studied to 27% in newly extruded larvae. This seems unusual in light of other values for teleosts, which range from 9 to 18% of total nitrogen (Niimi, 1972), and may be indicative of a nitrogenous source of maternal nutrition.

Comparing calorimetry and catabolic energy utilization provides evidence that additional maternal nutrition is provided during gestation. Based upon the calculation of 0.273 catabolic caloric necessary during gestation, 64.3% of the initial energy is used for catabolism. This suggests that the efficiency of yolk utilization from fertilization to parturition is approximately 36%. Calorimetry, however, shows that 81% of the initial energy investment remains at parturition. The difference represents energy from the maternal system. It is probable that the nutritional substance is nitrogenous, such as amino acids or peptides, since the total nitrogen remains nearly constant during gestation (Tables I, II). Comparing the time course of gestation and the energy content remaining as calculated by catabolism and calorimetry reveals the approximate times and developmental stages at which the nutrition is provided (Fig. 3). Energy content remaining after catabolism continued to decrease over development; measurements from calorimetry are similar through an embryonic age of about 20–25 days, corresponding to Oppenheimer stage 26.

The location of uptake of nutritional substances by embryonic *S. melanops* was approached from a structural standpoint, with examination of the epidermal surfaces and the histology of the alimentary tract. Epidermal uptake has been suggested for certain species and has been documented in the clinid *Clinus superciliosus* by Veith (1980). In embryonic *S. melanops,* we examined epidermal tissues at Oppenheimer stages 21, 31, and in larvae shortly after parturition, representing approximately 13, 29, and 38 days post-fertilization, respectively. At stage 21, prior to provision of maternal nutrients (Fig. 3), the epidermis on the nape (posterior to the cranium) and yolk sac regions is relatively smooth, with only cell boundaries distinct. Small, 3–4 μm depressions are apparent irregularly over the epidermis; these depressions may represent the locations of subdermal sacciform cells (Bullock, 1980). Only weak evidence of microridges, and no microvilli, are present (Fig. 4a). Epidermal microridges on stage 31 embryos are better developed in both nape (Fig. 4b) and yolk sac regions (Fig. 4c). In both of these developmental stages, relative development of the microridges decreases towards the tail. Finally in larvae shortly after birth, the microridges remain but are less distinct (Fig. 4d).

TABLE II

Comparison of protein, nitrogen, and carbon content from embryonic Sebastes melanops

Oppenheimer stage	Nitrogen (μg)	Carbon (μg)	Protein (μg)	PN/TN
9	7.30 (—)	41.64 (—)	45.27 (1.20)	0.99
23	7.78 (0.26)	40.71 (1.18)	46.27 (3.97)	0.95
28	7.64 (0.04)	38.48 (0.16)	36.23 (1.53)	0.76
Larvae at birth	7.74 (0.06)	34.42 (0.09)	35.31 (3.80)	0.73

Protein was determined using the methods of Itzhaki and Gill (1964) and carbon-nitrogen by CHN analyzer. Numbers in parentheses indicate one standard deviation. (PN/TN = ratio of protein nitrogen to total nitrogen.)

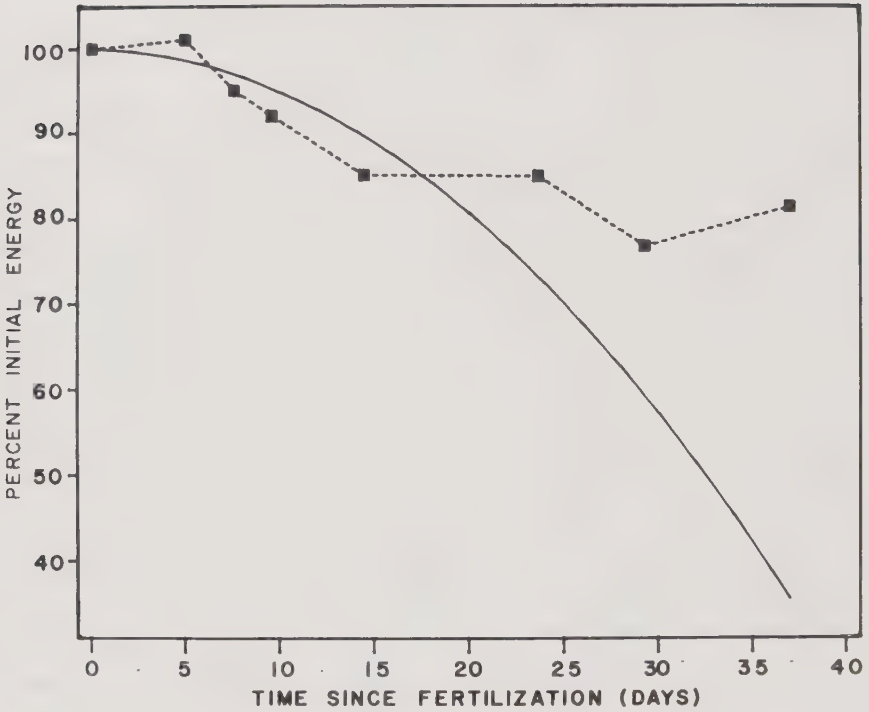

FIGURE 3. Comparison of energy budgets in embryonic *Sebastes melanops* during gestation based upon direct and indirect calorimetry. The dashed line represents caloric values of embryos at various times during gestation. The solid line represents energy utilization based upon the model of oxygen consumption during gestation and assumes an oxycalorific equivalent of 0.005 cal (μl O_2)$^{-1}$.

Histological observations on the gut of embryonic *S. melanops* demonstrate a change with increasing development. In early embryos, the foregut is not open, and the gut epithelium is relatively narrow and basophilic, with material lacking in the gut lumen (Fig. 5a). With development past stage 27, however, observation of whole embryos and serial sections show that the gut is open. Few histological changes are noted in either foregut or midgut regions, with the obvious exception of acidophilic material in the lumen (Fig. 5b). In the hindgut or rectum, however, the gut lumen also contains an amorphous substance and the height of the hindgut epithelium is greater. Additionally, there are large, supranuclear inclusions and some vacuolation (Fig. 5c). Finally, at stage 31, the hindgut epithelium is greatly expanded with marked increases of acidophilic supranuclear inclusions (Fig. 5d).

DISCUSSION

The reproductive mode in *Sebastes* has previously been termed "primitive" ovoviviparity (Amoroso, 1960; Wourms and Bayne, 1973; Wourms, 1981) despite a lack of experimental studies on this genus. The high fecundity, lack of structural modifications for embryonic nutrition, and small embryonic and larval size suggested that embryos received no nutrition beyond oogenesis. Our approach in this study has followed several studies on yolk utilization in oviparous species, and therefore comparisons of energy utilization are relevant here. Values useful for such comparisons

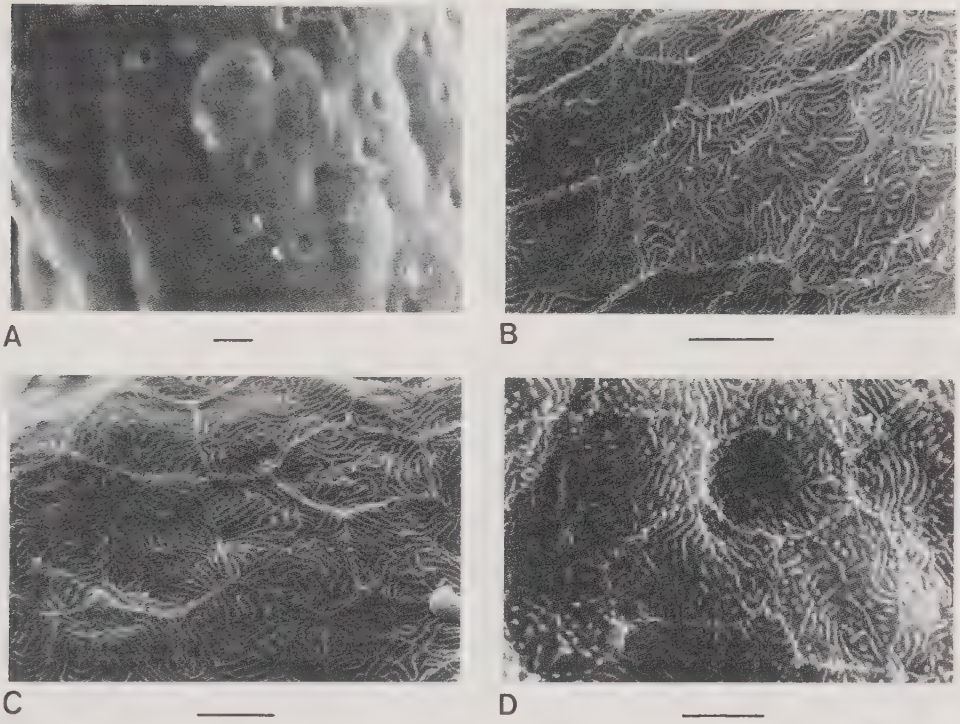

FIGURE 4. Scanning electron micrographs of the epidermis of embryonic and larval *Sebastes melanops*. a. Stage 21 embryo (13 days post-fertilization), nape region. Note the 3–4 μm depressions. Although the cell boundaries are distinct, the microridges are only poorly developed. b. Stage 31 embryo (29 days post-fertilization), nape region. c. Stage 31 embryo, yolk sac region. d. Larva shortly after parturition, nape region. Scale bars indicate 10 μm.

are the "plastic efficiency coefficient" (PEC) of Gray (1928) and the "apparent energetic efficiency" (AEE) of Needham (1931). The former is the ratio of dry weight of the developed embryo to that of yolk at fertilization, and the latter is the ratio of the caloric values of the same stages. Value of PEC and AEE from oviparous teleosts range from 0.24 to 0.65 and 0.26 to 0.79, respectively, and clearly demonstrate the expected decrease in mass and energy content during development (Table III). Among viviparous species, Thibault and Schultz (1978) noted values of PEC from 0.61 to 18.83 within the genus *Poeciliopsis;* their data suggest that *P. monacha* is a lecithotrophe, whereas the other three species receive varying levels of additional maternal nutrition during gestation.

Development in *Sebastes* shows some similarities to that in oviparous species. Oxygen consumption continually increases during gestation (Fig. 2), but the length of gestation is much greater than incubation time of equivalent sized eggs from oviparous species. Ware (1975), for example, compiled information on incubation times, sizes, and temperatures of marine species with pelagic eggs and demonstrated a highly significant relationship of egg diameter and incubation time. This relationship predicts an incubation time of 1.3 days given the egg size of *S. melanops* or an egg size of 4.4 mm given its incubation time; this is in marked contrast to the 37-day incubation and 0.8 mm egg size. The pattern of energy utilization described above also demonstrates important differences. The only prior information on *Sebastes,*

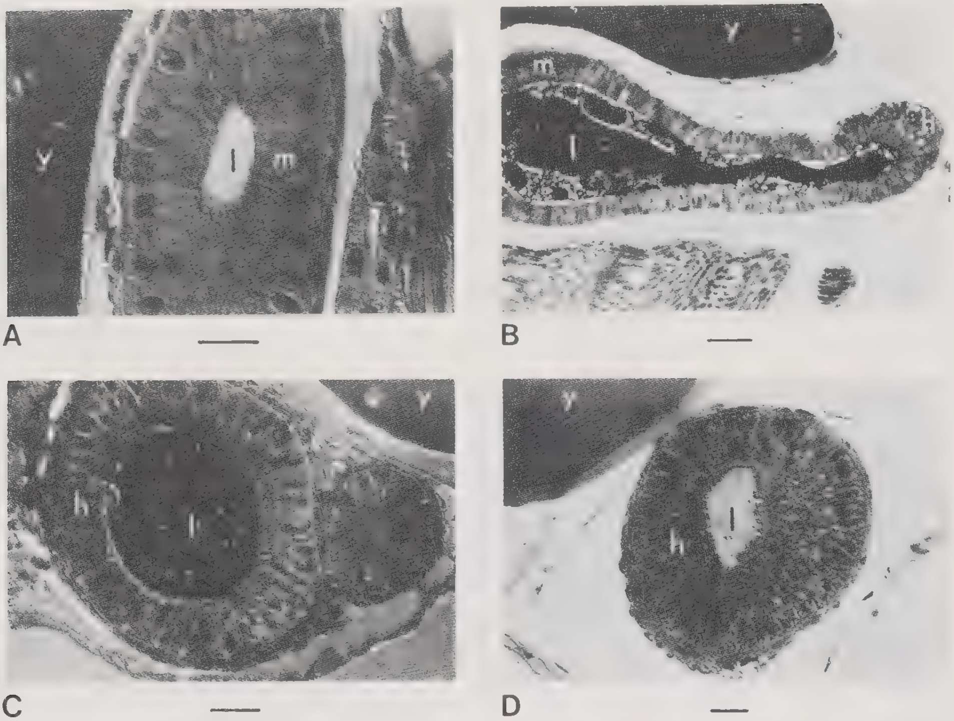

FIGURE 5. Histological sections of gut tissue in various stages of embryonic *Sebastes melanops*. a. Stage 21 embryo (13 days post-fertilization), midgut region dorsal to the yolk sac. Note the columnar gut epithelium and empty lumen (scale bar = 20 μm). b. Longitudinal section of the midgut-hindgut region of a stage 28 embryo (24 days post-fertilization). Note the densely staining, acidophilic substance throughout the lumen of the gut (scale bar = 50 μm). c. Cross section of the hindgut of a stage 28 embryo. Note the expanded hindgut epithelium with material in the lumen (scale bar = 20 μm). d. Cross section of the hindgut of a stage 31 embryo (29 days post-fertilization). The lumen contains an amorphous, granular substance, and the epithelial cells are characterized by supranuclear granules (scale bar = 20 μm). (h = hindgut epithelium; l = lumen; m = midgut epithelium; y = yolk sac.)

that of Hsaio (unpubl.), however, supports the idea of lecithotrophic viviparity in *S. marinus*. He demonstrated ". . . a pronounced fall in the dry weight of the developing egg, indicating little or no maternal contribution" (Needham, 1942). The only accessible data of Hsaio, however, are presented in Scrimshaw (1945), where the dry weight of the newly fertilized egg is presented as 0.003 g. This value is more than an order of magnitude greater than dry weights observed in the present study (Table I), and in Moser (1967a), which are in the range of 70–100 g. While the egg size in *S. marinus* is slightly larger than that of some Pacific species (Taning, 1961), it is doubtful that it could be 30-fold greater in dry weight. We therefore consider his unpublished values unreliable. Our value for PEC, 0.90, could conceivably be at the upper range of oviparous or lecithotrophic viviparous species (Table III). Furthermore, the value of AEE determined by oxgyen consumption is within the range of values determined for oviparous species. Relative to other species where both values are available, however, the relationship of the two values is inconsistent with the interpretation of lecithotrophic viviparity. Calorimetry demonstrates that the caloric content of the larva at parturition represents 81% of the initial energy invested at oogenesis. This value is more representative of that expected given the value of 0.90 for PEC. The sum of energy used

TABLE III

Efficiency of yolk utilization in selected fishes

	Temperature °C	PEC	AEE	Source
Oviparous species				
Tautoga onitis	16	0.41	0.36	Laurence, 1973
	19	0.29	0.26	Laurence, 1973
	22	0.30	0.26	Laurence, 1973
Congiopodus leucopaecilus	11.5	—	0.64	Robertson, 1974
Solea solea	10	—	0.68	Fluchter and Pandian, 1968
	15	—	0.55	Fluchter and Pandian, 1968
	20	—	0.47	Fluchter and Pandian, 1968
Limanda ferruginea	4–12	0.24–0.45	0.32–0.41	Howell, 1980
Paralichthys dentatus	16	0.61	0.62	Johns and Howell, 1980
Sardinops caerulea	14	0.48	0.79[1]	Lasker, 1962
Viviparous species				
Poeciliopsis monacha	22–32	0.61	—	Thibault and Schultz, 1978
P. lucida	22–32	1.34	—	Thibault and Schultz, 1978
P. prolifica	22–32	3.50	—	Thibault and Schultz, 1978
P. turneri	22–32	18.83	—	Thibault and Schultz, 1978
Sebastes marinus	—	0.66	—	Hsiao, unpub. (cited in Schrimshaw, 1945)
S. melanops	10	0.90	0.81 (0.36)[1]	Present study

PEC refers to the "plastic efficiency coefficient" (Gray, 1928) which is the ratio of dry weight of the developed embryo to that of the fertilized egg. AEE refers to the "apparent energetic efficiency" of Needham (1931), which is the same ratio using caloric values rather than dry weight. Values for viviparous species refer to embryos at parturition, when a small amount of yolk may remain.

[1] Utilization is based upon oxygen consumption and oxycalorific equivalents.

for catabolism (0.273 calorie) and that remaining at birth (0.345 calorie) represents 1.46 times that initially available at fertilization. A comparison of energy utilization during embryogenesis (Fig. 3) suggests that energy is first provided between Oppenheimer stages 22 and 28, corresponding to approximately 15 and 24 days after fertilization, respectively.

Viviparous teleosts display several adaptations for embryonic nutrition; the range of variation has been discussed in reviews on viviparity in fishes (Amoroso, 1960; Wourms, 1981). The most notable adapations for nutrient exchange are generally present in the embryonic, rather than maternal tissues. In some species, transfer of materials and respiratory gases may simply take place across the epithelium of the body and fins (Veith, 1979, 1980). In the embiotocids, the median fins become spatulate and highly vascularized, serving the function of respiratory gas exchange (Webb and Brett, 1972; Dobbs, 1975). Trophotaeniae are extensions of gut tissue present in several viviparous families which serve an absorptive function (Turner, 1937; Amoroso, 1960; Wourms and Cohen, 1975). These structures are continuous with the gut and assimilate ovarian secretions or histotrophe; similarly, other species may simply ingest ovarian fluid without externally specialized trophotaeniae (Dobbs, 1975; Veith, 1980).

In *S. melanops* embryos there are no notably specialized structures for uptake of histotrophe equivalent to those of more advanced viviparous species (Wourms and Bayne, 1973; Wourms, 1981). The epidermal structure of *S. melanops* embryos (Fig. 4) suggests that uptake does not occur there. Although there are numerous microridges which generally characterize teleost epidermis (Yamada, 1968; Depeche, 1973; Roberts *et al.,* 1973), microvilli usually characterize the absorptive surfaces on embryos of viviparous fishes, both on epidermal (Veith, 1980) and trophotaenial surfaces (Lombardi and Wourms, 1978). Veith (1980), for example, noted numerous epidermal microvilli situated on macroridges in early embryos of *Clinus superciliosus* and demonstrated uptake of labeled compounds via autoradiography. Uptake was limited to relatively small embryos, however, as the microvilli fused to form epidermal microridges later in gestation when the gut assumed the function of nutrient uptake. In *S. melanops,* the increased development of microridges with time after fertilization (Fig. 4) may be a response to increased oxygen consumption (Fig. 2), even after parturition, since larval fish epidermis often serves a respiratory function (Weihs, 1980).

The other possible site of nutrient uptake is the gut. Examination of gross morphology of embryos during gestation demonstrates that the mouth is open and the gut continuous at Oppenheimer stage 27, approximately 22 days post-fertilization. This time correlates well with the timing of maternal nutrition as estimated in Figure 3. Histological examination of the gut agrees with this assessment (Fig. 5). In early stage embryos, the gut epithelium is relatively narrow and basophilic (Fig. 5a), a condition similar to that described by Govoni (1980) for nonfeeding yolk sac larvae of *Leiostomus xanthurus.* With development past stage 27 in embryonic *S. melanops,* however, an amorphous acidophilic material is present in the lumen of the hindgut, evidence of ingestion of histotrophe (Fig. 5b, d); this may be similar to the material observed in the expanded hindgut of stage 28 *S. schlegeli* by Shimizu and Yamada (1980). This material is absent in earlier stages. Also the most marked change in the gut epithelium occurs in the hindgut, where the epithelium is characterized by marked expansion and development of supranuclear acidophilic inclusions and vacuolation (Fig. 5d). O'Connell (1976), in diagnosing the feeding condition of larval *Engraulis mordax,* used similar supranuclear, eosinophilic inclusion bodies in the hindgut to evaluate the relative nutritional state of larvae. Actively feeding larvae were characterized by "massive" supranuclear inclusions in the hindgut; his histological figures of this state are similar to those of later stage embryos of *S. melanops.*

Evidence for uptake of exogenous substances in the hindgut supports the idea that the substance is possibly amino acids, peptides, or proteins. Iwai (1969) suggested that protein is absorbed in the hindgut of larval fishes, largely by pinocytosis. This has been confirmed by Watanabe (1981, 1982), who described the uptake and intracellular digestion of horseradish peroxidase in the guts of larvae of several teleosts. The nitrogen content of developing embryos of *S. melanops* remains nearly constant (Table I) while protein decreases (Table II). In development of most oviparous teleost larvae, protein and nitrogen decrease during development. Rogers and Westin (1981) noted a decrease of 48% in total nitrogen in developing striped bass larvae and a marked increase in the carbon:nitrogen ratio, which contrasts with the decreasing ratio in *S. melanops* (Tables I, II). Similarly, Hayes (1949) suggested that 40% of the original yolk proteins in the trout egg are used as energy sources in development. Thus while other sources of nutrition cannot be ruled out, protein or other nitrogenous energy sources are clearly involved in additional maternal nutrition of embryos.

Although the basic reproductive pattern in the genus *Sebastes* is similar among species, variations in reproductive strategy and life history pattern exist. Variations in maximum size (and therefore fecundity), age at maturity, seasonality of spawning, multiple spawning, and longevity are well documented within the genus; furthermore, intraspecific variations may occur with latitude (Boehlert and Kappenman, 1980). Small species such as *Sebastes jordani* and *S. emphaeus* may mature at age 2, reach a maximum size of 179 mm (*S. emphaeus*) and maximum ages of about 7 years, and achieve maximum fecundity of approximately 50,000 developing embryos (Phillips, 1964; Moulton, 1975). Larger species such as *S. paucispinis* may mature at age 4 or later, reach maximum lengths of 870 mm, bear an annual or biannual brood of up to 2,300,000 developing embryos, and reach maximum ages of 30 years (Phillips, 1964; Moser, 1967a). Other investigators have documented ages greater than 80 years (Bennett *et al.,* 1982). Other species have not been studied relative to additional maternal contribution. The opaque substance in the enlarged rectum of *S. schlegeli* embryos noted by Shimizu and Yamada (1980), however, suggests a similar nutritional mode during gestation. Ultrastructural analysis of rectal cells of embryos in this species reveals that they are characterized by supranuclear inclusions similar to those noticed in *S. melanops* (Fig. 5d), also indicative of exogenous nutrition (M. Shimizu, pers. comm.). Thus the pattern of nutrition documented for *S. melanops* may occur in other species in this genus. Given the wide variety of over 100 species of *Sebastes* (Barsukov, 1981), however, there may be variability in maternal nutrition as is apparent within genera of other viviparous groups such as the poeciliids (Table III; Thibault and Schultz, 1978).

Viviparity in *Sebastes* is a significant adaptation to environmental conditions, as in other viviparous species (Amoroso, 1960; Wourms, 1981). Although Turner (1947) could draw no ecological correlations with reproductive type among the poeciliids, Thibault and Schultz (1978) suggested that the diverse reproductive mechanisms relate closely to conditions of predators, food availability, and physical environment. In marine fishes, most mortality is concentrated in the early life history during so-called "critical periods" (Hjort, 1914; Marr, 1956). In the Pacific sardine, for example, mortality may be 30% per day during the pelagic egg stage (Smith, 1973) and 10% per day during the larval stage (Lenarz, 1973). Thus brooding of embryos during development may significantly decrease early mortality due to predation and starvation. Further, less energy is necessary for protection of the embryo. In oviparous species, the chorion represent 15–33% of egg dry weight (Blaxter and Hempel, 1966; Robertson, 1974); in *S. melanops,* however, it represents only 1.6%. The protective function served by the chorion in oviparous species (Davenport *et al.,* 1981) is apparently unnecessary in the benign ovarian environment. The chorion in *S. paucispinis* embryos is only 1 μm thick and "porous" in nature (Moser, 1967b). It is probable that this chorion does not prevent movement of macromolecules, since exogenous nutrition of embryonic *S. melanops* occurs some 8 days prior to hatching from the chorion.

Within the family Scorpaenidae, seven of eight subfamilies are oviparous; only the Sebastinae is characterized by internal fertilization and viviparity. *Sebastes* is clearly the most advanced genus within this group, which also includes the genera *Hozukius* and *Helicolenus.* While the reproductive pattern of the deep-living *Hozukius* is unknown (Barsukov, 1981), *Helicolenus* is thought to be the most primitive (Krefft, 1961). While internally fertilized, *Helicolenus* lays gelatinous egg masses similar to those of the oviparous genera *Scorpaena* and *Sebastolobus;* larvae at parturition are in varying stages of development (Krefft, 1961; Graham, 1939). In the genus *Sebastiscus* (considered a subgenus of *Sebastes* by Barsukov and Chen, 1978) parturition occurs immediately after hatching in the ovary (Tsukahara, 1962). There has been some controversy concerning the stage of development at birth in *Sebastes,* but observations of natural birth generally support hatching within the ovary (Moser 1967b; Kusakari, 1978; present study). We estimate that 5 days elapse between hatching and birth for *S. melanops* at 10°C.

While *Sebastes* is the most reproductively advanced genus within the Scorpaenidae, it is generally considered primitive among viviparous fishes (Amoroso, 1960; Wourms, 1981). A primitive character present in the *Sebastes* female reproductive system is the presence of paired ovaries which are uncommon among viviparous species (Amoroso, 1960). A unique specialization in the reproductive system is the dual arterial system supplying fresh arterial blood to each ovary, which no doubt presents a relatiely high respiratory oxygen demand on the maternal system during embryogenesis (Moser, 1967b). It is interesting to note that the genera of the subfamily Sebastinae show morphological and osteological evidence for primitive and advanced characters which correspond to the degree of reproductive specialization; *Helicolenus* is most primitive and closest to the ancestral, oviparous scorpaenines, *Sebastes* is the most advanced (Krefft, 1961; Moser and Ahlstrom, 1978).

Kusakari *et al.* (1977) observed that the larvae of *S. schlegeli* at spawning are embedded in a gelatinous matrix which gradually dissolves after pectoral fanning by the female. Such a gelatinous substance is consistent with the gelatinous egg masses of *Helicolenus, Scorpaena,* and *Sebastolobus.* Wourms (1981) questioned whether this jelly in *Helicolenus* might play some trophic function. We have not observed spawning or such a viscous matrix in *S. melanops;* thus ovarian fluid may be a more fluid histrophe in this species. This histotrophe may be produced in the granulosa cells noted by Moser (1967b) to hypertrophy in *S. paucispinis* ovaries. A second source of histotrophe may arise from resorbed embryos which die during development. Boehlert *et al.* (1982) observed degenerating embryos in fertilized *S. entomelas* ovaries and noted decreased fecundity with later developmental stages in this species. In the latter case, if embryonic death occurs, the energy contained in these embryos may be recovered by brood mates.

Reproductive similarities among genera in the subfamily Sebastinae and relationships with other genera in the family suggest that evolution of viviparity proceeded through progressively longer retention of developing embryos. In the ancestor of extant sebastines, internal fertilization was probably followed by rapid deposition of fertilized embryos (Barsukov, 1981), a condition termed ovi-ovoviviparity by Balon (1975). In *Helicolenus* retention time of fertilized embryos may be variable (Krefft, 1961), with eggs deposited shortly after fertilization, or retained for longer periods (Graham, 1939). *Sebastes* larvae, on the other hand, are typically ready to feed at birth, with organogenesis complete. Thus evolution of viviparity in the scorpaenids involved progressively greater commitments of parental care; additional nutrition from ovarian fluid, or histotrophe, may have simply developed as an "opportunistic and passive strategy" (Wourms, 1981). It would thus be interesting to investigate the range of variability in viviparity for the genus *Sebastes.*

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VARIABILITY IN AGE ESTIMATES IN *SEBASTES* AS A FUNCTION OF METHODOLOGY, DIFFERENT READERS, AND DIFFERENT LABORATORIES [1]

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Age was determined in the fast growing canary rockfish, *Sebastes pinniger,* and the slow growing splitnose rockfish, *S. diploproa,* by different laboratories, techniques, and readers. Variability between agencies depended upon method and species. For *S. pinniger* aged by both laboratories, whole otolith ages were similar, whereas the otolith section ages greatly exceeded those of whole otolith ages. Clear differences were noted for the slower growing *S. diploproa;* whole otolith ageing methods differed between the two laboratories, with much greater ages for larger specimens assigned by one laboratory. These older whole otolith ages showed similarities to the otolith section ages for this species, but still did not reveal the longevity noted with sections. We suggest two areas where improvement in precision of age determination is necessary. First, a consensus on ageing methodology (whole versus sectioned or broken and burned otoliths) is necessary to allow meaningful comparisons between readers. Secondly, mechanisms to allow comparisons between agencies or laboratories are necessary to provide ages which are, at the least, consistent, for use by fisheries managers.

INTRODUCTION

Using otoliths to define annuli and estimate age in fishes is difficult for several reasons. For fast growing species with clear otoliths, a consensus of different readers on age may be obtained, but for longer-lived species, age determination becomes more difficult and subjective (Williams and Bedford 1974, Maraldo and MacCrimmon 1978). The genus *Sebastes* is characterized by species with a great range of longevity, from maximum ages of about 4 to 5 years in *S. emphaeus* (Moulton 1975) to in excess of 80 years in several deeper living species (Beamish 1979*b*; Bennett, Boehlert, and Turekian 1982). In the longer-lived *S. marinus* and *S. mentella,* Sandeman (1961) noted only 9% agreement between readers; as expected, variability between readers increased with increasing age.

Different methods may also produce different results; ageing of *Sebastes* spp. has been conducted with scales (Phillips 1964), whole otoliths (Westrheim 1973, Boehlert 1980), and otolith sections (Beamish 1979*b*). Westrheim and Harling (1973) compared whole otolith versus scale methods for *S. alutus* and noted older ages from otoliths. Bias between readers in the same laboratory, using the same methods, is likely to be less than between agencies or laboratories (Kimura, Mandapat, and Oxford 1979). If, as on the Pacific coast, several agencies routinely age the same species, problems may arise for management in interpretation of the appropriate ages to use.

Whole otoliths are commonly used by management agencies in assessing age structure of a population. Several studies have indicated that a certain amount of bias is introduced with this method, especially where older individuals of the species are concerned. Growth of an otolith is a function of age as well as length of the fish. The otolith increases in length up to a given size of fish, after which it ceases to increase in length or width but continues to increase in thickness with age (Blacker 1974, Templeman and Squire 1956). This thickening occurs on the internal surface of the otolith, particularly in slow-growing, long-lived species. Relying solely on whole, surface ageing of the otolith's external surface will therefore neglect this cap of additional material. Certain investigators have found that using a section from an otolith reveals these internal banding patterns and suggest maximum ages which are double or even triple those estimated with whole otoliths (Sandeman 1961, Beamish 1979*a* and 1979*b*); that these older ages represent true ages has been demonstrated for *Sebastes diploproa* using natural radionuclides in otoliths by Bennett *et al.* (1982). Because management agencies are currently reassessing ageing techniques for rockfishes, a comparison of some of the alternative ageing methods and the variability within and between methods is desirable. In the present study we investigate deviations in estimated age of *S. diploproa* and *S. pinniger* as a function of different readers, different laboratories, and different methodologies.

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MATERIALS AND METHODS

Sebastes diploproa and *S. pinniger* were sampled at depths from 32 to 205 fm by the chartered vessels F/V PAT SAN MARIE and F/V MARY LOU during the 1980 West Coast Groundfish Survey conducted by the Northwest and Alaska Fisheries Center, National Marine Fisheries Service. Gear, sampling techniques, and shipboard methods generally followed Gunderson and Sample (1980).

Sagittal otoliths were collected from fish captured in all hauls until sufficient numbers of specimens in specified length categories were obtained; very large and very small individuals thus represented a higher proportion in our sample than in the population. Specimens were numbered consecutively, as taken, within sexes. Vessel, leg, haul, sex, and fork length (to the nearest 0.1 cm) were recorded for each specimen. Additional information on each haul included latitude, longitude, and bottom depth. Both otoliths were removed, cleaned, and stored in individual, labelled vials containing 50% ethanol.

General information on otolith morphology and whole otolith ageing methodology in *Sebastes* is described in detail by Kimura *et al.* (1979). Whole otoliths for both species in our study were read with a dissecting microscope at 10x under reflected light. Otoliths were immersed in water on a black background. Generally, the best area to read was on the exterior surface of the whole otolith, from the focus to the dorsal edge. With fish older than approximately 12 yrs, a prominant annulus was followed to the posterio-dorsal or posterior region, where subsequent annuli were counted due to compression of annuli in the dorsal area. With older fish, particularly for *S. diploproa,* the whole otolith was rolled or tilted to enumerate annuli on the outer-most projections in the posterior region (Figure 1).

A single whole otolith age was determined for each specimen of *S. diploproa* by Oregon State University (OSU) reader A and *S. pinniger* by OSU reader B. Fish length remained unknown to all otolith readers, as recommended by Williams and Bedford (1974), among others, to minimize bias in otolith reading. A second whole otolith age was assigned approximately ten weeks after the initial age assignments to determine within-reader differences. Further, for *S. diploproa,* whose otoliths are more difficult to read, one additional whole otolith age was determined by OSU reader C for an estimate of between-reader variability within an agency. After these ages were determined the entire sample of each species was sent to a different age reading laboratory (reader D) to establish inter-agency variability in whole otolith ages.

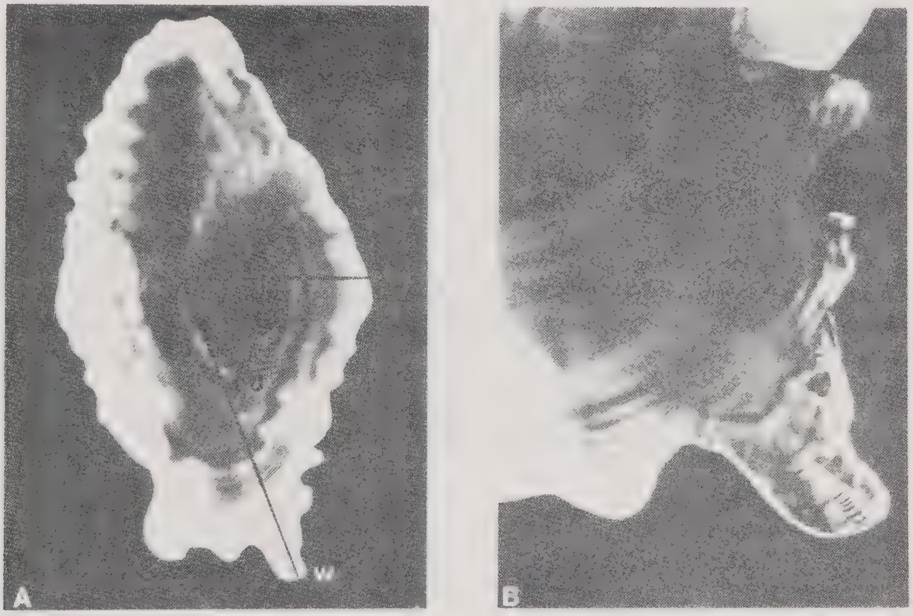

FIGURE 1. A. Exterior surface of the left otolith from a 308 mm FL male *Sebastes diploproa* (8X). The whole otolith age from OSU is 32 yrs. Readings were made from the focus to the dorsal edge (d — axis), continuing along a prominent annulus around to the posterio-dorsal (pd) axis. B. Enlarged portion of the posterior projections (w), showing additional annuli not apparent on the dorsal axis (32X).

The left otoliths of both species were subsequently prepared and sectioned as described by Boehlert (1984). Annuli of specimens younger than approximately 20 yrs were counted on a dissecting microscope using either transmitted or reflected light. The narrow annuli in otoliths from older fish were discerned using transmitted light on a compound microscope at approximately 10x. The ages were determined from the transmitted image on a video screen, for ease of enumeration on older fish. Annuli on the dorso-ventral axis, from the focus to the dorsal edge, are often split on otolith sections, making it difficult to identify the first several true annuli. For this reason, 25 whole left otoliths from *S. pinniger* and 50 from *S. diploproa* were selected, and distance was measured from the focus to accepted annuli (complete rings surrounding the focus) for approximately the first eight years. These measurements were used to identify the location of corresponding annuli on the same axis of the sectioned otolith and showed that our interpretation of annuli was similar between methods for young fish. By following these annuli to the internal, dorsal surface, only a single growth zone was observed, as noted by Sandeman (1961); checks or false annuli found on the whole otolith either disappear or combine on this axis. Section ages were subsequently determined as described in Beamish (1979*b*). Section ages for both species were determined twice for each specimen by OSU reader A, approximately one month apart.

Since true age is not known with certainty for any otolith, initial whole ages determined by reader A for *S. diploproa* and by reader B for *S. pinniger* were considered as "standard age". Initial section ages by reader A in both species were considered "standard". To conduct multiple comparisons of variability, deviations from standard age were defined as shown in Table 1, where group 1 is the difference between independent ages determined by reader A for *S. diploproa* and by reader B for *S. pinniger,* group 2 (for *S. diploproa*) is the difference between standard whole age and that determined by reader C, group 3 compares standard whole otolith age with the age determined by reader D, group 4 is the difference between independent section ages determined by reader A, group 5 is the difference between standard section and standard whole otolith ages, and group 6 is the deviation of reader D whole age from standard section age. Deviations were normally distributed. A one-way analysis of variance (ANOVA) was used to compare these deviations for each species and sex. Multiple range testing was conducted using the Least Significant Difference method (p = 0.05) (Tables 2, 3, 4, 5).

TABLE 1. Identification of the Deviations of Standard Age to Define the Groups in Statistical Comparisons of Deviations.

Group	*Group definition*
1	whole otolith within-reader variation
2	between reader variation (*S. diploproa* only)
3	inter-agency variation
4	section within-reader variation
5	between-method variation
6	between-method-between-agency variation

TABLE 2: Results of One-Way Analysis of Variance and Multiple Range Test Comparing Deviations in Age of *Sebastes Diploproa* Females Determined by Different Readers and Methods. (Groups are defined in text and in Table 1.)

Analysis of Variance

Source	*D.F.*	*Sum of squares*	*Mean squares*	*F*	*P*
Between groups	5	6912.87	1382.57	41.78	<.001
Within groups	1718	56854.99	33.09		
Total	1723	63767.86			

Group	*N*	*Mean*	*Standard deviation*
1	290	0.217	2.018
2	290	−0.728	3.697
3	282	3.206	6.028
4	290	−0.024	2.156
5	290	2.007	6.711
6	282	4.993	9.831

Multiple range test (Least significant difference, P = .05)

Group 2 Group 4 Group 1 Group 5 Group 3 Group 6

TABLE 3: Results of One-Way Analysis of Variance and Multiple Range Test Comparing Deviations of Age in *Sebastes Diploproa* Males Determined by Different Readers and Methods. (Groups are defined in text and in Table 1.)

Analysis of Variance

Source	*D.F.*	*Sum of squares*	*Mean squares*	*F*	*P*
Between groups	5	7784.99	1557.00	36.97	<.001
Within groups	1466	61733.50	42.11		
Total	1471	69518.49			

Group	*N*	*Mean*	*Standard deviation*
1	246	−0.138	1.907
2	246	−0.537	2.669
3	244	2.598	4.972
4	246	0.126	2.445
5	246	3.427	8.595
6	244	5.865	11.746

Multiple range test (Least significant difference, P = .05)

Group 2 Group 1 Group 4 Group 3 Group 5 Group 6

TABLE 4: Results of One-Way Analysis of Variance and Multiple Range Test Comparing Deviations of Age in *Sebastes Pinniger* Females Determined by Different Readers and Methods. (Groups are defined in text and in Table 1.)

Analysis of Variance

Source	*D.F.*	*Sum of squares*	*Mean squares*	*F*	*P*
Between groups	4	1345.59	336.40	46.72	<.001
Within groups	600	4322.49	7.20		
Total	604	5668.08			

Group	*N*	*Mean*	*Standard deviation*
1	121	−0.050	0.717
3	121	1.413	1.838
4	121	0.017	3.152
5	121	2.455	3.209
6	121	3.868	3.449

Multiple range test (Least significant difference, P = .05)

Group 1 Group 4 Group 3 Group 5 Group 6

RESULTS

Sebastes diploproa

The sample of *S. diploproa* otoliths was comprised of 290 female and 246 male specimens. This sample was representative of the age, length, and latitudinal distribution of otoliths described in Boehlert (1984). Standard whole otolith ages ranged from <1 to 56 yrs for female and 1 to 40 yrs for males. Length frequencies and corresponding age distributions resulting from the various sources of age estimation were tabulated (Table 6). Females were generally more abundant in the large size categories. Mean ages-at-length, both for the females and males, showed distinct differences when comparing whole otolith age estimates from different laboratories. Mean OSU ages were consistently lower than the other agency for the smaller, younger fish and were higher for those older and larger fishes (Table 6).

TABLE 5: Results of One-Way Analysis of Variance and Multiple Range Test Comparing Deviations of Age in *Sebastes Pinniger* Males Determined by Different Readers and Methods. (Groups are defined in text and in Table 1.)

Analysis of Variance

Source	*D.F.*	*Sum of squares*	*Mean squares*	*F*	*P*
Between groups	4	8779.49	2194.87	101.66	< .001
Within groups	850	18350.47	21.59		
Total	854	27129.96			

Group	*N*	*Mean*	*Standard deviation*
1	171	−0.029	0.747
3	171	−0.310	2.812
4	171	0.836	3.665
5	171	6.813	7.065
6	171	6.503	6.011

Group 3 Group 1 Group 1 Group 4 Group 6 Group 5

Reader variability in all comparisons generally increased with increasing fish length (and therefore age), and was greatest for older, larger females. The mean deviation in whole otolith ages between agencies as a function of whole standard age for both male and female *S. diploproa* (Figure 2) was much greater than either within or between reader differences within one laboratory. Up to age 10 for both sexes, OSU ages were more conservative than those of the other laboratory, resulting in negative deviations. After age 10, OSU whole ages were increasingly greater, up to a mean maximum deviation of about 30 yrs for the oldest females and 19 yrs for males. The negative deviations at younger ages could result from different interpretations of assumed annuli; OSU readers identified only complete rings as annuli, as compared with false annuli or checks, for the first several years of growth, although the first growth bands are admittedly difficult to interpret. The deviations at older ages are due to the inclusion of annuli on the posterio-dorsal projections of the otolith in the OSU age estimates (Figure 1).

Otolith section ages for *S. diploproa* were generally greater than whole otolith ages. Within-reader deviations for otolith section ages were similar to within and between-reader whole age deviations. Deviations were great when comparing section and whole ages. For both males and females, the mean deviations of whole from section ages at OSU were low for the first 30 yrs and began to diverge after this age (Figure 3). Maximum deviations were greater for males than for females (51 yrs and 29 yrs, respectively). Females grow faster than males and their otoliths are clearer. Annuli are easier to discern for older females on the surface of the whole otolith. The deviations of whole age from section age are therefore smaller in females. Moreover, from whole otolith estimates, females appear to be older than males, whereas maximum ages estimated from sectioned otoliths reveal an opposite trend (66 yrs for females and 74 yrs for males).

Inter-agency differences between standard OSU section age and whole age from another laboratory as a function of standard section age (Figure 4) showed a pattern similar to that for section-whole deviations within an agency, with a few important exceptions. Mean deviations at ages greater than 10 yrs are greater in the inter-agency comparison and are negative at ages less than 10 yrs. This further emphasizes the difference in ageing criteria used between laboratories. In addition, the deviations diverge from zero at a much lower age; that is, divergence is at 10 yrs for inter-agency and 30 yrs for within-agency comparisons, reflecting the older whole otolith ages determined by OSU.

Sebastes pinniger

This study utilized 121 female and 171 male *S. pinniger* otoliths. As with *S. diploproa*, females were more abundant in the largest size categories (Table 7), apparently due to their faster growth rate (Boehlert 1980, Boehlert and Kappenman 1980). Standard whole ages ranged from 2 to 22 yrs for females and 2 to 25 yrs for males. Mean ages-at-length were generally higher for OSU estimates when compared with the other agency (Table 7).

Otoliths of *S. pinniger* are generally clearer, easier to read, and this species does not reach the ages attained by *S. diploproa*. As expected, mean interagency differences in whole otolith ages were minimal when compared with those of the more difficult to read *S. diploproa* otoliths. Moreover, although section ages were generally greater than whole ages, the magnitude of this deviation was not as great as that observed for *S. diploproa*. This reflects the greater clarity and ease in surface reading of *S. pinniger* otoliths (Figure 5).

Mean within-reader differences were similar in both whole and section age comparisons. Inter-agency differences between OSU standard section age and whole age from the laboratory were similar to within-agency differences of the same comparison; this results from closer estimates of whole ages between agencies. Considering this comparison (between methods), deviations were high but less than those for *S. diploproa*. Maximum between-method deviations, from OSU as well as the other laboratory, were higher for the slower growing, longer-lived males, as observed for *S. diploproa*.

One-way analyses of variance demonstrate significant differences between the sources of deviations in age for both males and females of both species of *Sebastes* (Tables 2,3,4,5). Multiple range testing suggests that mean within-agency sources of deviation for *S. diploproa* (including within-reader for both whole and section ages and between-reader) are similar and significantly less than inter-agency deviations. Consequently, precision in age determination can be high among readers within one laboratory, but can decrease greatly when comparing ages between laboratories. These results also suggest that precision is highly dependent upon the method used in age determination, with comparisons of ages derived through different methods by different laboratories resulting in the greatest deviations.

TABLE 6. Mean Ages-at-Length for Different Readers and Methods of Age Determination in *Sebastes diploproa*.

A. Female (N=290)								*B. Male (N=246)*							
		Whole otolith age				*Otolith section age*				*Whole otolith age*				*Otolith section age*	
Length (cm)	*N*	*A1*	*A2*	*C*	*D*	*A1*	*A2*	*Length (cm)*	*N*	*A1*	*A2*	*C*	*D*	*A1*	*A2*
13	1	2.0	2.0	3.0	4.0	2.0	2.0	9	1	1.0	1.0	1.0	3.0	1.0	1.0
14	2	2.0	2.0	2.5	4.5	2.5	2.5	11	1	3.0	3.0	3.0	4.0	4.0	4.0
15	4	3.5	3.5	3.5	4.5	3.3	3.3	12	1	1.0	1.0	1.0	3.0	1.0	1.0
16	5	3.8	3.2	4.8	5.0	3.4	3.6	13	1	1.0	1.0	1.0	3.0	1.0	1.0
17	5	4.4	4.0	5.4	5.2	4.2	4.4	14	2	3.5	3.5	4.0	5.0	3.5	1.5
18	7	5.1	4.3	5.7	5.4	5.3	5.1	15	5	4.0	2.8	4.2	4.8	4.2	5.6
19	8	5.5	5.4	6.4	5.9	5.6	5.5	16	3	4.0	4.0	3.7	4.7	4.0	4.0
20	11	6.2	6.1	7.1	6.0	6.0	6.1	17	3	5.0	4.7	5.7	5.3	6.0	6.0
21	15	6.3	6.3	6.9	6.9	6.8	6.3	18	8	5.0	4.9	5.6	6.4	5.9	5.5
22	12	6.9	6.6	7.9	7.2	7.6	7.5	19	7	5.3	5.0	5.9	6.0	5.4	5.7
23	24	7.4	7.3	8.1	7.3	7.5	7.3	20	11	5.5	5.4	6.1	6.1	5.7	5.8
24	19	7.4	6.9	7.7	7.3	7.5	7.7	21	16	7.0	6.7	7.0	6.9	6.9	6.9
25	13	8.3	8.2	9.5	8.1	10.8	10.5	22	23	7.2	7.1	7.6	7.2	7.3	7.6
26	25	9.2	9.4	10.3	9.0	9.6	9.1	23	22	7.7	7.6	8.2	7.4	7.9	8.0
27	23	9.4	10.1	10.1	9.2	9.3	9.3	24	16	8.9	8.4	9.1	8.2	9.1	8.9
28	10	12.3	11.6	12.0	11.1	11.4	11.3	25	13	8.4	8.4	9.4	9.4	8.7	8.9
29	16	16.6	16.3	16.9	12.6	17.3	17.6	26	24	9.6	9.1	9.8	10.0	9.6	9.6
30	17	23.1	23.4	22.1	15.6	22.9	23.2	27	13	14.2	13.6	14.2	10.8	14.5	14.9
31	15	23.5	25.1	25.3	17.0	25.7	26.1	28	13	19.5	18.4	19.5	13.9	23.4	20.5
32	8	28.1	30.0	32.0	21.5	30.4	31.3	29	17	26.7	27.4	27.4	19.1	32.6	34.1
33	11	30.1	30.2	33.2	20.1	39.6	40.2	30	15	26.1	26.5	28.9	18.3	33.1	31.3
34	9	32.9	36.8	36.7	22.6	48.9	48.3	31	12	29.0	28.9	28.1	16.9	43.3	43.1
35	7	39.1	39.0	34.9	23.5	42.9	40.7	32	14	30.2	31.4	31.2	20.1	49.1	48.2
36	15	38.3	39.1	38.7	22.2	48.9	49.6	33	3	25.7	25.7	29.7	14.0	47.3	46.7
37	7	38.1	37.0	34.9	24.7	40.1	42.0	34	1	30.0	31.0	35.0	19.0	54.0	57.0
38	1	36.0	38.0	48.0	18.0	62.0	63.0	36	1	32.0	30.0	33.0	22.0	68.0	69.0

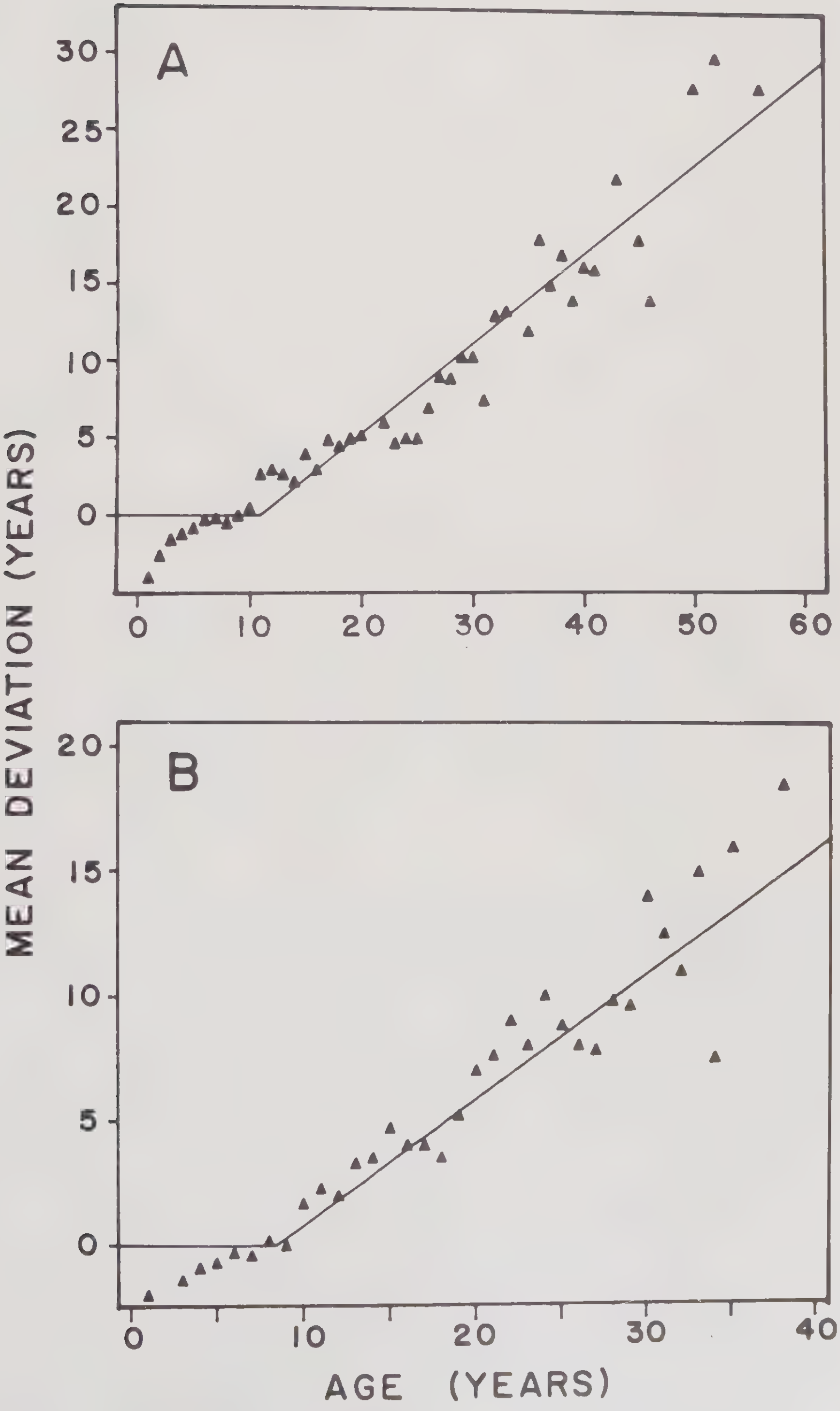

FIGURE 2. Mean deviations in whole otolith ages between agencies for splitnose rockfish, *Sebastes diploproa*. A. Females (N = 290). B. Males (N = 246).

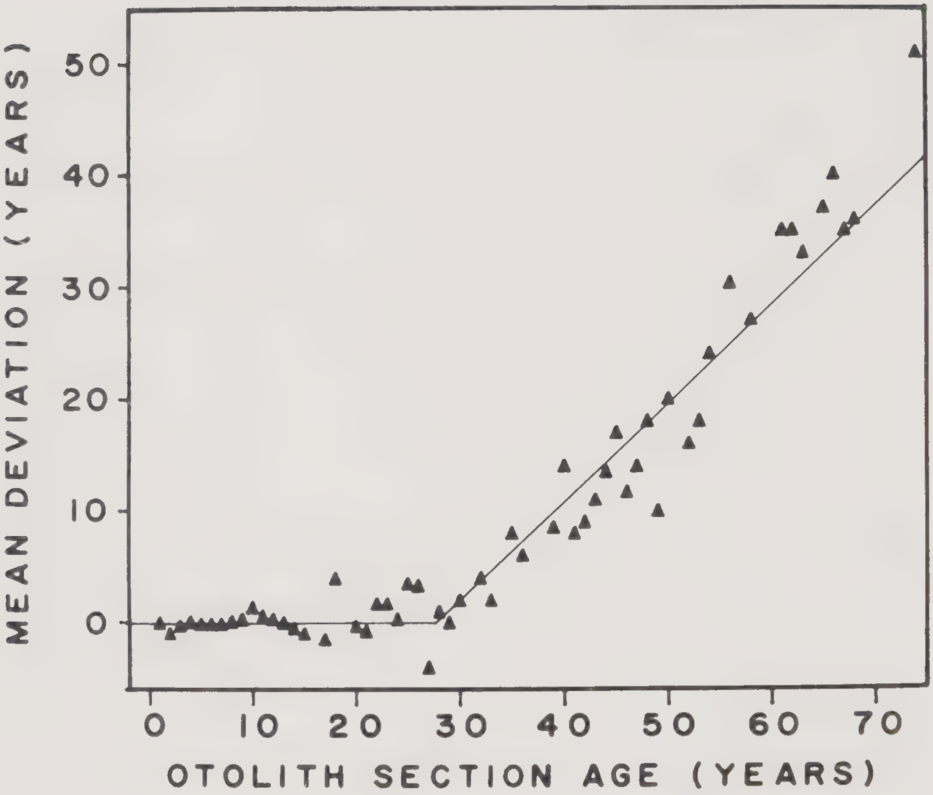

FIGURE 3. Mean deviation of OSU whole otolith age from otolith section age for male *Sebastes diploproa* (N = 246).

For *S. pinniger,* multiple range testing demonstrated similar trends, with deviations in age being greatest when comparing methods both between and within agencies. Inter-agency deviations are relatively low, however, when comparing whole ages from these clear, easy-to-read otoliths.

DISCUSSION

This study does not conclude that assigned ages are accurate, since age validation is beyond the scope of this study. It does suggest that age determination using whole otoliths will not adequately represent the age of most *S. diploproa* beyond 30 yrs and *S. pinniger* beyond age 10 yrs. Section ages seem to more accurately define the age composition of a population, particularly in the case of longer-lived species with difficult-to-read otoliths (Bennett *et al.* 1982). It would therefore be beneficial to examine otoliths from other species of rockfish to determine at what age, if any, it becomes necessary to section the otolith to estimate the true age of the fish. A method which provides results similar to sectioning is the break and burn technique, as described by Chilton and Beamish (1982). This technique, which also involves examination of an otolith cross section, may be more amenable to production-type age determination than the sectioning methods used in the present study. In the genus *Sebastes,* however, it is apparent that these greater ages exist in a wide variety of species (Shaw and Archibald 1981).

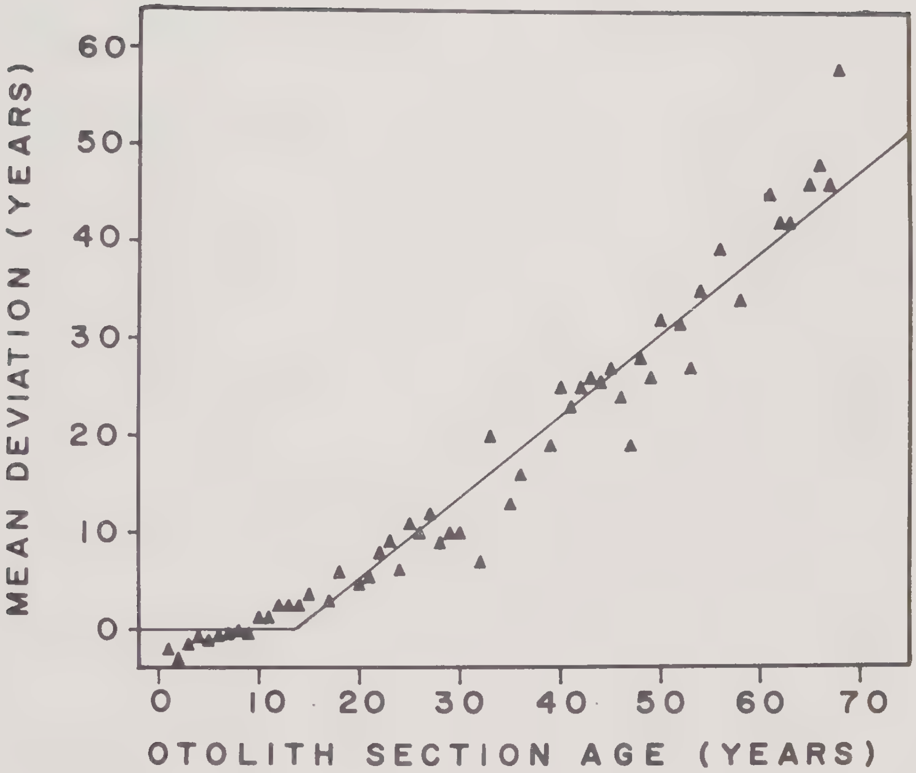

FIGURE 4. Differences between otolith section ages and whole otolith ages from another agency for male *Sebastes diploproa* (N = 246).

It is clear from our results that an important part of the populations of both species is significantly underaged using the whole otolith technique, particularly by the other laboratory (Figures 3,4,5). An important point to note from these data is the fact that the deviations for males are generally greater than those for females. Female *Sebastes* grow faster than males for most species (Boehlert and Kappenman 1980, Westrheim and Harling 1975) and are therefore characterized by otoliths which have broader, clearer annuli on whole otoliths to a greater age. Thus, the age at which the otolith growth occurs only as "caps" on the internal surface will be greater for females. Using whole otoliths for age determination, the females will appear to be older than the males whereas the opposite is actually true based upon section age (Tables 6 and 7). The systematic bias which is introduced by using whole otolith ages is therefore compounded by differences in the error of longevity estimates for males and females.

These older fish represent an important part of the population which should not be ignored. Hirschhorn (1974) argued that excluding older, difficult-to-age individuals from growth analysis for the population can have detrimental effects upon estimates of von Bertalanffy parameters. For production modelling or stock analysis purposes, unbiased errors in age determination, particularly for older segments of the population, will have little effect, whereas systematic bias in

TABLE 7. Mean Ages-at-Length For Different Readers and Methods of Age Determination in *Sebastes pinniger*.

A. Female (N=121)

Length (cm)	N	Whole otolith age			Otolith section age	
		B1	B2	D	A1	A2
15	1	2.0	2.0	2.0	2.0	3.0
31	1	5.0	5.0	4.0	7.0	7.0
32	2	5.5	5.0	3.5	7.0	7.0
33	1	4.0	4.0	3.0	3.0	4.0
36	1	9.0	9.0	8.0	13.0	12.0
37	1	7.0	7.0	6.0	8.0	8.0
38	3	7.0	7.3	6.3	8.3	10.7
39	1	6.0	6.0	5.0	6.0	6.0
41	3	8.0	8.0	7.7	10.3	10.3
42	2	9.5	9.5	8.0	10.5	10.5
43	2	8.0	8.0	7.5	11.0	11.0
44	1	9.0	9.0	8.0	10.0	9.0
45	2	11.0	11.0	10.0	12.0	13.5
46	5	11.0	11.4	9.0	11.4	11.8
47	4	11.0	11.0	8.0	12.5	10.5
48	7	11.9	12.0	11.1	12.7	13.0
49	8	11.8	12.0	10.5	12.3	13.4
50	5	11.2	11.4	10.8	12.6	16.4
51	10	12.8	12.7	11.2	15.6	14.9
52	9	13.1	13.1	10.7	14.9	13.9
53	18	13.6	13.6	12.2	16.8	16.6
54	6	13.5	13.8	12.8	16.0	15.8
55	8	15.4	15.3	14.1	18.5	17.6
56	9	15.7	15.2	13.8	19.9	19.6
57	5	14.6	14.8	12.6	19.4	19.6
58	2	16.0	16.5	15.5	17.0	15.5
59	1	16.0	16.0	16.0	28.0	27.0
60	1	17.0	16.0	11.0	15.0	26.0
61	2	18.5	20.0	17.0	30.5	26.5

B. Male (N=171)

Length (cm)	N	Whole otolith age			Otolith section age	
		B1	B2	D	A1	A2
17	1	2.0	2.0	2.0	2.0	3.0
20	1	3.0	3.0	3.0	3.0	3.0
22	1	3.0	3.0	3.0	3.0	4.0
23	1	3.0	3.0	3.0	4.0	5.0
28	1	5.0	5.0	5.0	6.0	6.0
34	2	7.0	7.0	6.5	8.5	8.0
37	2	6.0	6.0	4.0	7.0	8.0
38	1	7.0	7.0	5.0	9.0	8.0
39	1	8.0	8.0	8.0	13.0	10.0
40	5	8.0	8.0	7.8	9.2	9.6
41	2	7.5	7.5	7.0	8.5	12.5
42	4	8.3	8.3	6.5	7.8	9.3
43	4	10.3	10.5	8.0	12.5	14.8
44	4	9.5	9.5	9.5	11.3	13.5
45	4	12.5	12.5	9.8	15.3	18.5
46	7	11.6	11.9	10.9	15.1	16.7
47	16	11.8	11.8	11.4	15.1	15.4
48	9	13.0	12.9	13.2	15.7	16.4
49	13	12.8	13.5	13.8	18.0	18.3
50	25	13.3	13.4	13.7	19.2	20.6
51	14	15.1	15.3	16.2	26.4	27.7
52	18	15.5	15.4	15.8	25.3	25.9
53	17	17.3	17.0	19.5	29.6	29.8
54	7	15.9	16.0	17.9	28.9	29.4
55	4	18.8	18.8	19.5	33.3	30.8
56	2	18.5	18.0	21.5	43.0	50.5
57	4	18.8	18.8	17.8	29.8	29.0
58	1	16.0	15.0	15.0	32.0	25.0

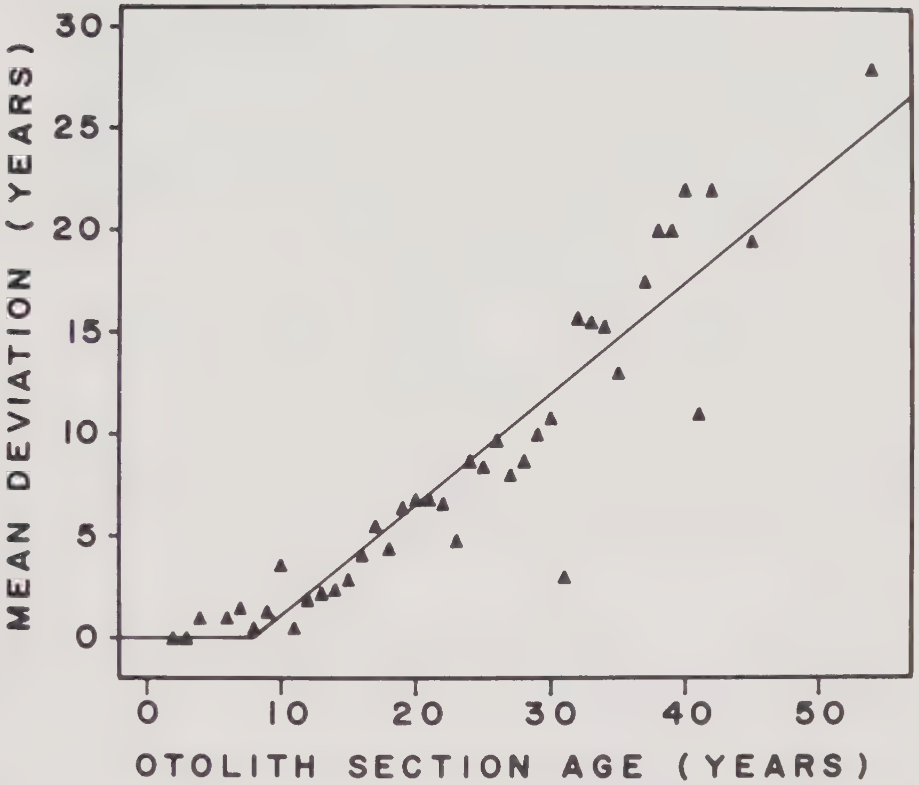

FIGURE 5. Differences between section age and whole otolith age determined by another agency for male *Sebastes pinniger* (N = 171).

ageing may give rise to serious errors (LeCren 1974). Thus, the systematic errors introduced by using ages determined from whole otoliths will negatively affect production models. Calculations of both natural and fishing mortality will clearly be in error, and use of such age data in cohort analysis or virtual population analysis will result in inaccurate cohort strength estimates.

It is difficult to define the causes of the systematic error between agencies. Some error may arise from method alone. Use of different magnifications, for example, may result in different visibility of annuli. Reading otoliths with transmitted versus reflected light, in aqueous media versus dry, or other minor changes in method may result in such systematic differences. Methodological problems will be easiest to solve. Differences in interpretation are more difficult to address. Ages determined within agencies may show high precision and repeatability, but differ significantly from ages at another agency. This suggests that training and frequent cross-checking can solve the problems between agencies.

This study represents an effort to consider the errors inherent in ageing rockfish based upon reader variability, method variability, and agency variability. We concur with Kimura *et al.* (1979), that variability among agencies is greater than that between readers in the same laboratory. We suggest that significant effort be placed upon minimizing variability between agencies. A necessary first step to this goal will be standardization of methods and equipment for ageing each species. Within each species, common interpretation of criteria for defining annuli must be developed. Achieving this goal will initially take a great deal of uniform training and interagency calibration. Continued communication among otolith readers of different agencies, while expensive in time and travel, will ultimately result in more effective fisheries management.

ACKNOWLEDGMENTS

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USE OF ULTRASONIC TELEMETRY TO DETERMINE THE SHORT-TERM MOVEMENTS AND RESIDENCE TIMES OF TUNAS AROUND FISH AGGREGATING DEVICES

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I. The importance of fish aggregating devices

The ability of floating objects to attract fish in the open ocean has long been recognized (reviewed by Seki, 1983). This phenomenon is now being exploited throughout the Pacific by the use of anchored buoys (referred to as fish aggregating devices or FADs) which are specifically designed to attract commercially important fish species (Shomura and Matsumoto,1982). Pioneering work by the Southwest Fisheries Center Honolulu Laboratory of the National Marine Fisheries Service (NMFS) has clearly demonstrated the benefits (e.g., increased catches, less travel time, and reduced fuel consumption) FADs provide to commercial and recreational fishermen (Matsumoto et al., 1981).

There has been research to determine effective FAD designs with respect to maintaining FADs on station for long periods (Boy and Smith, 1983) and increasing the ability of FADs to aggregate targeted species (Wickham et al., 1973; Wickham and Russell, 1974). There have also been studies on the feeding habits of FAD associated tuna and the changes in tuna feeding habits caused by FADs (Brock, 1984). However, little is known about the optimal placement of FADs with respect to oceanographic or bathymetric conditions, or to each other. Also, there is little or no direct information available on the true effects of FADs on the behavior of commercially important fish species or the ultimate impact of FADs on fishery resources. We therefore decided that much could be learned about the optimal placement and effects of FADs by using ultrasonic telemetry techniques to determine the short-term (1-12 days) behavior around FADs of commercially important fish species such as tunas. Yellowfin tuna, _Thunnus albacares_, and skipjack tuna, _Katsuwonus pelamis_, are the primary FAD associated target species in the Pacific (Matsumoto et al., 1981; Shomura and Matsumoto, 1982).

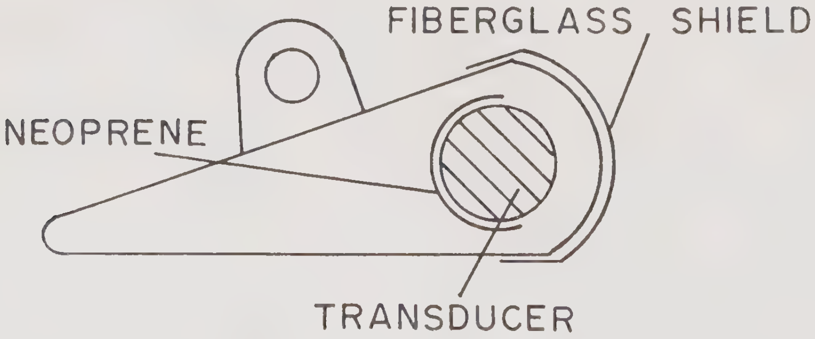
II. Description of the telemetry system

To monitor the fish's swimming depth, as well as their daily movements and residence times around FADs, we decided to employ depth sensitive ultrasonic transmitters. Transmitters, purchased from VEMCO[1] (Shad Bay, Halifax County, Nova Scotia), were 1.6 cm in diameter and either 7.4 or 8.0 cm long. The former weighed 28.8 g in air and 14.0 g in seawater and had a battery life of 2.2-3.7 days. The latter weighed 27.7 g in air and 11.7 g in seawater and had a battery life of 14-24 days. The 50 kHz carrier signal was 153-158 dB (re 1μ Pascal at 1 m), which gives the transmitters a working range of approximately three-fourths nautical mile in our system. Depth (water pressure) is measured with a strain gauge mounted on one end of the transmitter. The strain gauge controls the frequency of the transmitters' pulsed output, which ranges from approximately 1 per second at the sea surface to approximately 3 per second at 400 m. The transmitters are designed such that pulse frequency is linearly proportional to depth.

The directional hydrophone employed was also from VEMCO. The transducer and a preamplifier (50 dB gain) are mounted in a PVC housing. The hydrophone has a sensitivity of 144 dB (re 1 V/μ Pascal at 1 m), a horizontal acceptance angle (beam width) of 30°, and a vertical acceptance angle (beam width) of 150°.

Because of the high speed swimming abilities of tuna (Yuen, 1966), the pursuit boat has to intermittently travel at 7-8 knots for short periods while tracking. The directional hydrophones, however, are designed and are usually used for tracking much slower species. Therefore, the hydrophone had to be modified for our purposes. Directionality in the hydrophone is attained by a sheet of sound absorbing neoprene placed around a portion of the hydrophone's transducer element (Fig. 1). However, water pressure on the face of the transducer element, when the hydrophone is being rapidly moved through the water, compresses the neoprene and allows the transducer element to rotate. This can sever the wires connecting the transducer to the preamplifier in the body of the hydrophone. We lost a yellowfin tuna that we had been tracking for 5 hours before we discovered this weakness in hydrophone design. This problem was corrected by simply gluing the neoprene in place.

FIGURE 1 Side View of the VEMCO Directional Hydrophone Showing the Relative Positions of the Transducer, Sound Absorbing Neoprene and Fiber Glass Shield



In addition, a fiber glass shield was fitted over the face of the hydrophone (Fig. 1). The shield was made by impregnating fiber glass cloth with resin and then draping it over a PVC pipe of the proper diameter as the resin hardened. If care is taken so that no air bubbles are trapped in the fiber glass cloth, the shield is acoustically transparent. The shield improves the performance of the hydrophone at high boat speeds because it reduces water turbulence at the face of the transducer and increases the signal-to-noise ratio.

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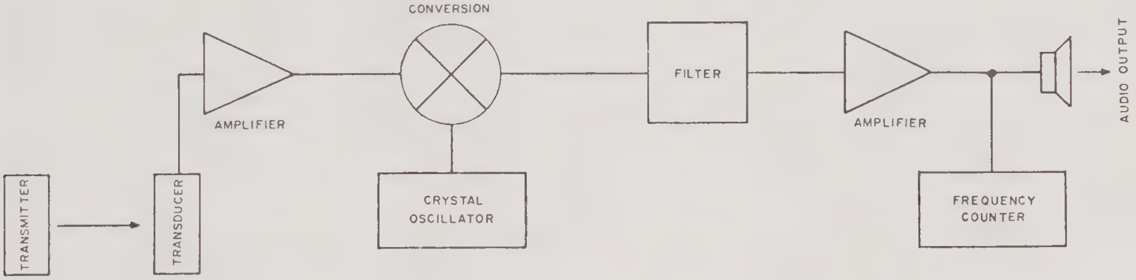
[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The ultrasonic receivers employed were Communication Associates (Huntington Station, NY 11746) model CR 40. The hydrophone-receiver system functions as follows. The hydrophone detects and amplifies the ultrasonic transmitter's signals plus background noise. In the receiver, a crystal controlled oscillator (designed to match the crystal controlled oscillator controlling the 50 kHz carrier frequency of the ultrasonic transmitter) is used to select the frequency to be converted to the audible signal. The strength of the audible signal is used by the boat operator to keep the directional hydrophone pointed at the fish. In other words, when the hydrophone is pointed directly at the fish the audible signal is louder than when the hydrophone is pointed in a slightly different direction. We recorded the audible signal with a Sony TCS-310 tape recorder and also fed the signal to a Telonics (Mesa, AZ 85201) TDP-2 frequency counter. This latter device displays pulse interval which, as stated, is inversely proportional to the fish's swimming depth. This swimming depth data were also recorded manually every 15 min. The Sony tape recorder was chosen because recorders of this type are designed for playback of recorded music and generally exhibit wow and flutter (a measure of the accuracy of tape speed) of approximately 1°/oo. Therefore, the tape recorder introduces no significant error with respect to shoreside analysis of the telemetered depth data. The entire telemetry system is shown schematically in Figure 2.

FIGURE 2 Diagram of the Ultrasonic Receiver System. The Tape Recorder (Not Shown) Is Connected Directly to the Audio Output



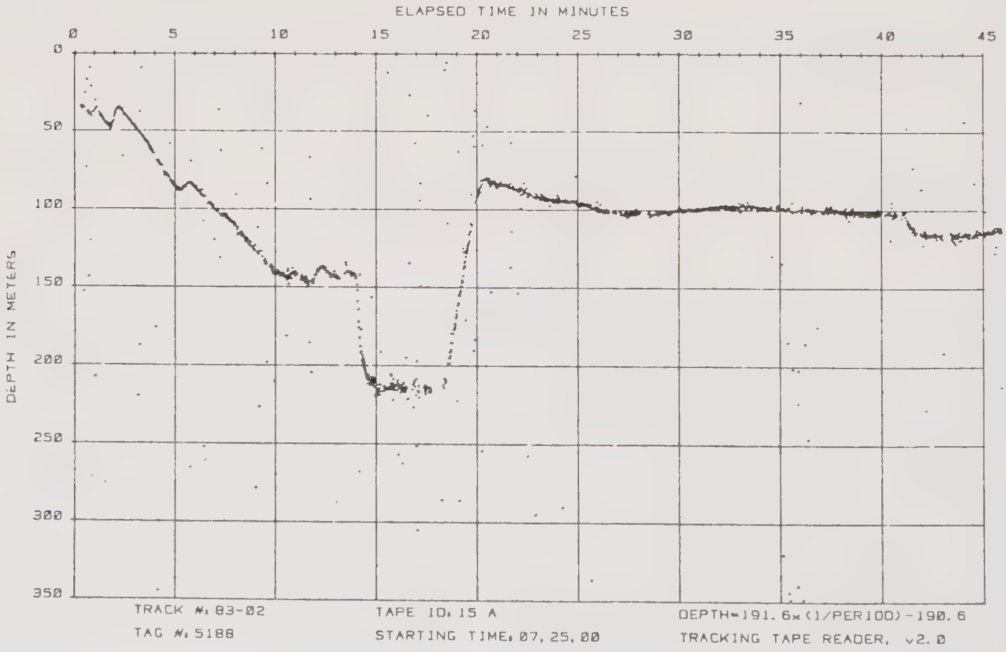
We employed a relatively small boat (11 m long) as a pursuit vessel, rather than the larger NMFS's research vessel that had been used for previous telemetry studies (Dizon et al., 1978). A small vessel has several advantages. First, it is relatively inexpensive to operate and it can be dedicated to this one project. Therefore, tracking can be attempted whenever conditions are optimal. Second, a small vessel is maneuverable enough so that the hydrophone can be fixed-mounted in one direction. Therefore, instead of turning the hydrophone to determine the location of the fish, the whole boat is turned. This greatly simplifies the mounting of the hydrophone on the boat and makes the whole structure more reliable. Third, and perhaps the most important, our 11-m boat is about the same size as the majority of the other vessels fishing around FADs in Hawaii. Our vessel, therefore, does not interfere with other vessels fishing near the FADs, as would a large fisheries research ship. Finally, the small boat is ideal for catching the relatively small tuna 50-70 cm fork length) that are suitable for tracking.

Small boats do have disadvantages. First, 120 V a.c. must be supplied by a small generator which is generally unstable with respect to alternating current frequency. This makes it difficult to operate computers and other sensitive digital electronic devices. Also, an 11-m vessel is subject to far more motion than is a large fisheries research ship and all areas of the boat are exposed to salt and moisture corrosion. A small boat is therefore not a suitable environment for sensitive digital electronic equipment. Finally, an 11-m vessel can only support a three- to four-man crew. Therefore, it is limited to a maximum tracking duration of approximately 48 hours before the crew must be exchanged. Our vessel does carry 290 gal of fuel, which at speeds used during tracking, provides enough fuel to track a fish for at least 3-4 days.

Because of the limitations of an 11-m vessel, the data acquisition system was designed with a philosophy of simplicity and (whenever possible) redundancy with respect to all critical and automated data acquisition equipment. Because of the amount of data that can be collected on the fish's swimming depth, automated data collection and computer analysis are needed. However, real time computer collection and analysis with a shipboard computer is not practical on a small vessel.

As described, we recorded the audible signal from the ultrasonic receiver with a Sony tape recorder. The tapes are then played back at our shoreside laboratory and every other pulse interval is plotted as a point on a depth-time graph. A Hewlett-Packard (HP) 9825A computer, an HP 5312A timer-counter (to measure pulse intervals), and an HP 7245A plotter-printer are used. This system permits one to determine spurious data points within the swimming depth data. Spurious depth data points can easily be seen in an example of the plotted depth data (Fig. 3).

FIGURE 3 Forty-five Minute Record of the Swimming Depth of a Yellowfin Tuna, Thunnus albacares. The Data Were Plotted by Computer Directly From the Tape Recorded Signal From the Depth Sensitive Transmitter



This system was chosen to get rid of spurious data points rather than a computer algorithm, such as that developed by Westerberg (1983), because our system requires the investigator to look at the data and forces the use of human judgment.

Furthermore, if the transmitter's signal begins to get out of range, although still audible to the boat operator, the signal-to-noise ratio can be insufficient to trigger the HP counter-timer. As shown in Figure 3, even when data plotting is intermittent, the fish's swimming depth pattern can easily be determined by eye and the missing data points filled in. Totally automated data processing would not permit this. We are in the process of developing computer programs to digitize and manipulate this plotted depth data by tracing the depth-time plots on a digitizer tablet.

Navigational data are collected in two ways. The first is by use of standard loran-C receiver (Furuno, model LC80) aboard the pursuit vessel. However, loran-C navigation is not consistent near the main Hawaiian Islands. Because tuna can be caught relatively near shore in the Hawaiian Islands, we are also able to determine vessel position by taking hourly fixes on landmarks using a hand-held compass. These land fixes are used to adjust the position information determined by loran-C. The tracking vessel's course is plotted by hand using both sources of position information.

III. Horizontal and vertical movements of yellowfin tuna around fish aggregating devices

Fish to be tracked are caught by trolling feather and plastic and rubber jigs. Heavy rods and reels are used to bring the fish to the boat as quickly as possible. The fish are then wedged in a trough lined with foam rubber which does not allow the fish to struggle excessively. A wet cloth is used to cover the fish's eyes which also helps to quiet the animals.

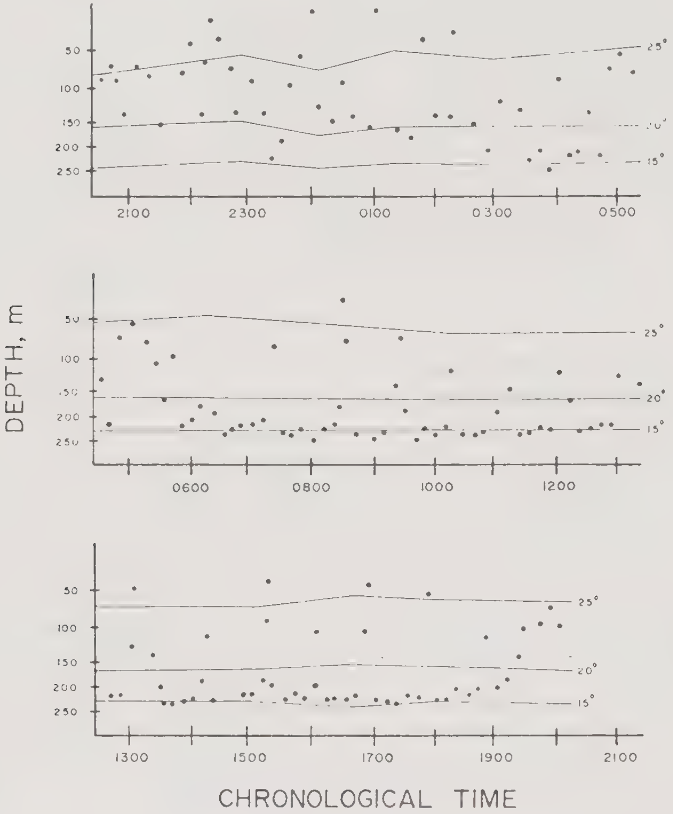
The transmitters are attached to the dorsal surface of the fish, posterior to the second dorsal fin. Plastic "tie wraps" are inserted through the muscle with the aid of hollow brass needles. One tie wrap is placed through a plastic loop on one end of the transmitter. A second tie wrap is used to hold the body of the transmitter to prevent it from flopping as the fish swims. Using this attachment method, dummy transmitters were placed on kawakawa, *Euthynnus affinis*, held at the Kewalo Research Facility of the Honolulu Laboratory, NMFS. These fish were able to carry the dummy transmitters for several weeks and swam, fed, and behaved normally.

So far we have been able to track three yellowfin tuna and one bigeye tuna, *T. obesus*. The use of a small dedicated pursuit vessel and a three-man crew has proven to be overwhelmingly successful. As Figure 3 shows, we are able to get long-term, yet fine scale, records of the fish's swimming depth.

Analysis of the data collected so far has revealed remarkable diurnal changes in both vertical and horizontal movements of tuna. A striking example of the former is shown in Figure 4, which is a plot of the swimming depth of a bigeye tuna recorded at 10-min intervals. The animal tended to remain nearer the surface at night and to descend to the depth of the 15°C isotherm (200 m) during daylight hours making only occasional forays to the surface during this time. The fish returned to its shallower swimming depth as the sun set (1900).

We have also observed instances of predictable diurnal rhythmicity in the horizontal movements of tunas. On one occasion this rhythmicity allowed us to relocate a yellowfin tuna on two separate occasions over a 5-day period. Similar behavior has been shown for skipjack tuna (Yuen, 1970). The practical advantage of these predictable horizontal movement patterns is that it is feasible to get extended tracks of tuna using a small pursuit vessel which can rapidly return to the nearest small harbor, refuel, exchange crews, and then return and relocate the fish carrying the transmitter.

FIGURE 4 Twenty-four Hour Record of the Swimming Depth of a Bigeye Tuna, *Thunnus obesus*. The Fish's Swimming Depth Was Recorded Manually Every 10 Min.



IV. Conclusions

Because of the rapidly increasing deployment of FADs throughout the Pacific, the cost of their deployment, and the use of and increasing dependance upon FADs by commercial and recreational fisheries, an understanding of the optimal placement and the true effects of FADs on fish and fishery resources is needed. Ultrasonic telemetry appears to us to be a rapid and relatively inexpensive way to gather some of the required information.

We have shown that with appropriate equipment, a small pursuit vessel can be used for open ocean tracking studies. We feel our system is both effective and efficient. We plan to continue our telemetry work for at least several more years and eventually we hope to track other pelagic species such as skipjack tuna and mahimahi (dolphinfish, *Coryphaena hippurus*) around FADs.

Acknowledgments

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Like whalers of old, the crew scans the horizon, searching for a glimpse of fins cutting the water. Then comes a cry from the starboard observer, "I've got dolphins at 37°!"

The crew swings into motion, glad for some action after hours of staring at an empty skyline. The action for this crew involves not longboats and harpoons, but high-powered binoculars and computers. These are research scientists out to answer a difficult question: "How many dolphins live in the 5 million square miles of the eastern tropical Pacific?" Environmentalists, biologists, and tuna fishermen would all like to have an accurate answer, for each of these groups has a stake in the "numbers game" that governs dolphin conservation practice.

In 1972, dolphin conservation was initiated as part of the Marine Mammal Protection Act (MMPA), a federal law that imposed a moratorium on taking and importing marine mammals or their products, with exceptions, in the United States.

One of the major exceptions is the dolphins. Because some species of dolphins often travel in association with schools of commercially valuable yellowfin tuna, dolphins are some-

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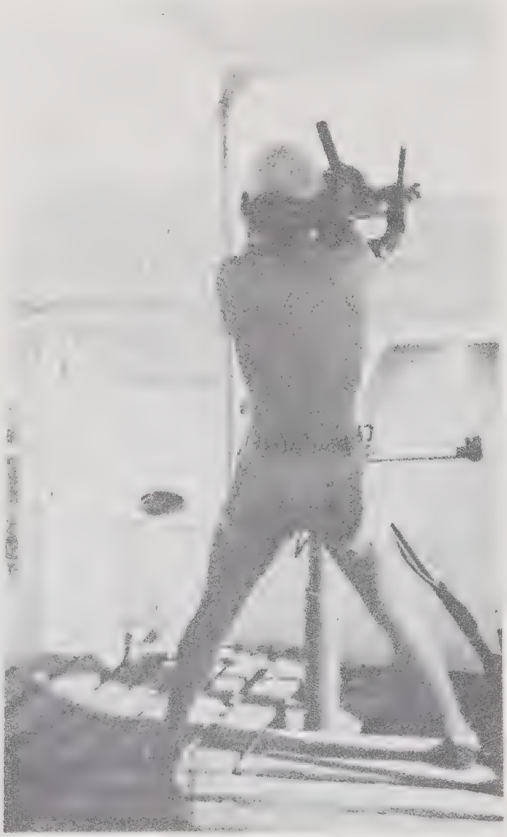
5 million square miles=13 million square kilometers

Previous page: Exploding *into action, these spinner dolphins (*Stenella longirostris*) leap from the water in apparent* joie de vivre. *Their characteristic runs of long low jumps punctuated with high leaps and midair spins allow these dolphins to be easily identified and counted.*

M. Scott Sinclair/NMFS



High-powered binoculars *are used to scan the sea for schools of dolphins. This vigil continues from sunup to sundown as* David Star Jordon *crisscrosses the eastern tropical Pacific. Two bottlenosed dolphins (*Tursiops truncatus*) are sighted and recorded in the log.*

Stephen B. Reilly/NMFS
Far right: M. Scott Sinclair/NMFS

times the incidental victims of tuna purse-seine operations. The MMPA acknowledges this tuna-dolphin relationship, and permits a limited amount of dolphin "take" — accidental death or serious injury — by the tuna fishermen.

Reduced mortalities

Great effort on the part of the U.S. tuna fishermen and the development of specialized gear and fishing techniques have combined to decrease the number of dolphin deaths: in 1977, more than a quarter of a million dolphins were killed or seriously injured during the tuna-fishing operations of U.S. boats; by 1979, the number of deaths had dropped to around 25,000, and has remained near 20,000 over the last several years.

While the take of dolphins by U.S. fishermen has declined dramatically, there is still concern among a number of scientists and environmentalists that the survival of some species and stocks of dolphins may be threatened if *any* incidental killing is allowed. The MMPA therefore designates certain species and stocks of dolphins as depleted and prohibits the killing or collecting of these animals.

The job of determining which dolphin stocks should be classified as depleted, and what the limit on take levels should be, falls to the Department of Commerce (DoC). Acting on information provided by research sci-

entists of the National Marine Fisheries Service (NMFS), DoC officials set annual limits on the number of dolphins that can be incidentally killed by fishermen, collected by research scientists, or permanently removed from the wild by commercial groups for public display.

To make their recommendations, NMFS researchers must first determine how many dolphins there are and how fishing and removals have affected the size of the dolphin populations. Counting the number of dolphins in an area the size of the eastern tropical Pacific has posed an ongoing challenge to scientists from the NMFS Southwest Fisheries Center at La Jolla, California. For the past six years, the scientists studying dolphin population size have been developing and refining their assessment techniques, trying to find the best method for counting the animals.

Computerized binoculars

In summer 1983, the La Jolla scientists "road-tested" their latest development, a method known as Computer Assisted Sighting Technique (CAST). CAST combines two sets of high-powered binoculars (strong enough to sight dolphins up to 6 miles away), a group of experienced dolphin observers, and a shipboard computer to form a system designed to give scientists the most accurate data yet available on dolphin distribution and population size.

Researchers on board the National Oceanic and Atmospheric Administration ship *David Starr Jordan* spent three months in the eastern tropical Pacific using CAST to collect precise measurements of the position of dolphin schools. Each morning, just after first light, the six observers would begin their search, taking turns on the binoculars throughout the day. The observers were responsible for identifying the species of dolphins that made up each school sighted (there are more than 15 dolphin species in the area), as well as the approximate size of the school and its position. Using a statistical formula known as the line-transect method, scientists can "plug in" this information to calculate the population density in a given area.

At one point in the trip, 20 dolphin schools were seen in a single day, while at other times hours would pass without a sighting. The researchers assume a patchy distribution of dolphin schools when making their final calculations of population density. Because they choose the survey area without respect to dolphin distribution, the scientists assume that they are measuring a set of events — dolphin sightings — that accurately represent a bigger picture—total dolphin population size and distribution. They can thus survey a small, randomly chosen section and use the sightings made in the survey area to project population figures for a much larger region.

As the research ship travels along a predetermined track line, or transect, observers using CAST record each sighting of a dolphin or school of dolphins. To calculate the density of the population, the researchers need to know three things: the number of dolphins found along the track line

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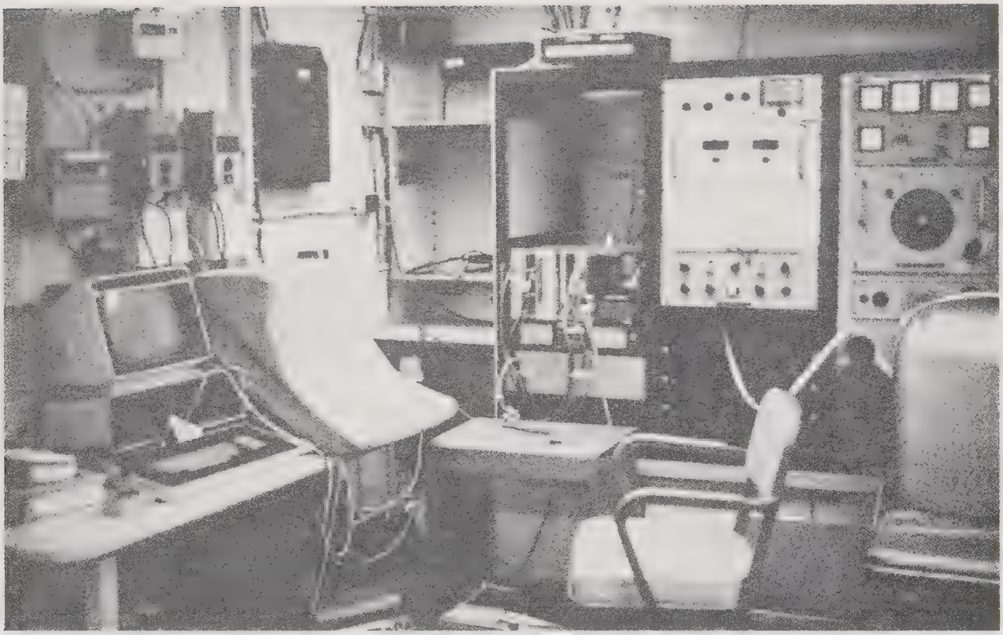
6 miles = 9.6 kilometers

Stephen B. Reilly/NMFS

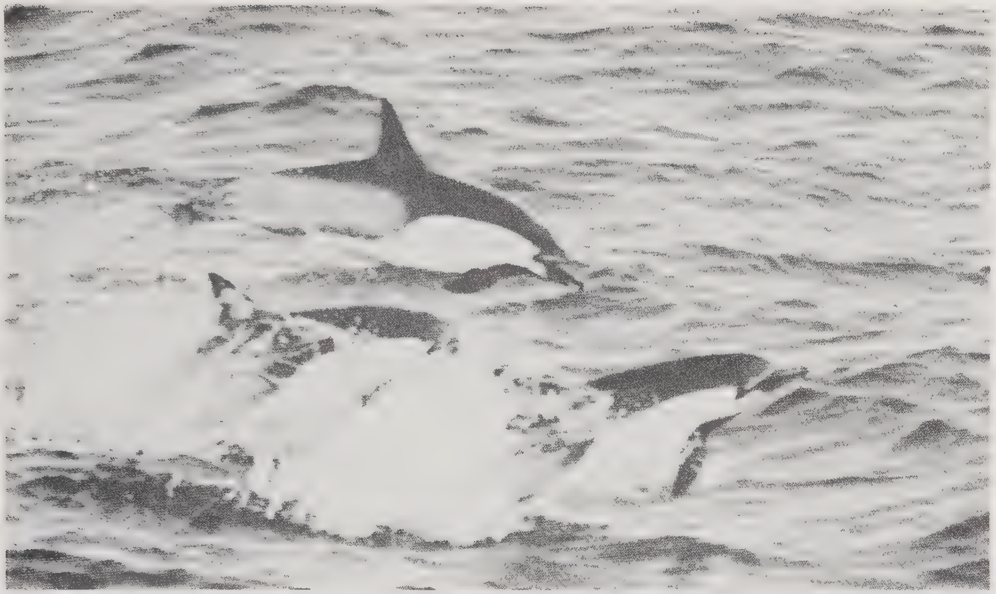


SOPHISTICATED COMPUTER *equipment aboard the ship instantaneously records the position of each dolphin school when either observer on deck indicates a sighting. The area of sea actually searched by the observers is also calculated.*

itself, the number of dolphins found at some distance from the track line and, in these cases, when the dolphins are not on the track line, the perpendicular distance from the position of the animals to the track line. The scientists can calculate that perpendicular distance if they know the sighting angle, defined as the angle between the ship's line of travel and the line of sight to the dolphins' position at the moment that the animals are detected by an observer, and the direct distance from the ship to the school.

The line-transect method is not a new technique—biologists have been using it for years to calculate everything from the number of trees per acre of forest to the number of duck nests per acre of marsh. But measuring the density of a dolphin population presents some unique challenges.

"One problem is that dolphin schools don't sit still," says Dr. Rennie Holt, one of the scientists involved in the dolphin-counting project. "We've therefore had to modify the line-transect technique, and measure a number of sighting angles to take into account the movement of the animals; using the resulting 'family' of lines, we can back calculate to get an accurate initial sighting angle," explains Holt. This sighting angle is the key to the formula — knowing the



PLAYFUL ACROBATICS *and distinctive markings of the common dolphin (*Delphinus delphis*) allow for easy recognition. The spotted or bridled dolphin (*Stenella attenuata*) is usually seen swimming near the surface rather than jumping high into the air.*

M. Scott Sinclair/NMFS

sighting angle means being able to calculate population densities.

In the past, measuring the sighting angle was a fairly crude procedure. "We used to collect angles and distances by just eye-balling the measurements, using the horizon as our guide," says Holt. "Then we went to a system where a notched washer was mounted on the binocular stand, and the observers would count off the clicks made by the swiveling binoculars as they panned away from the track line; the number of clicks gave an indication of the sighting angle. CAST uses an electronic encoder, again mounted on the binocular stand, which monitors the movement of the binoculars and feeds that information into the ship's computer. When the observer makes a sighting, he or she pushes a button, and the computer records the angle of the sighting by measuring the position of the binoculars. We can get very precise calculations of sighting angles that way."

The computer monitors not only the sighting angle, but the actions of the observers themselves. According to Holt, density measurements depend on observers seeing every animal located on the track line. As the observer pans out from the line, chances of spotting all the dolphins in the area decrease, a factor that the line-transect formula takes into account. The two observers, one on the port binoculars and one on the starboard set, are supposed to search only on their side of the track line. A formula in the computer determines whether or not the observers are actually looking where they are supposed to look.

The computer can also screen out the interference caused by the movement of the ship as sighting angle measurements are being taken. The computer records the number of degrees that the ship moves up or down (pitch), or from side to side (roll), then eliminates those changes to give an accurate reading of the sighting angle.

Months of analysis

Analyzing the computer data from the most recent monitoring cruise will take a number of months, but Holt is confident that CAST will provide the best information ever collected on dolphin population density.

In 1985, DoC officials will establish a new set of regulations on dolphin conservation practices for 1986 and beyond. The development and use of the CAST system represent an important advance in providing scientists with the most complete and accurate data on which to base an assessment of the status of the dolphins in the eastern tropical Pacific. □

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TEMPERATURE-INDUCED CHANGES IN BLOOD GAS EQUILIBRIA IN THE ALBACORE, *THUNNUS ALALUNGA*, A WARM-BODIED TUNA

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SUMMARY

Samples of unbuffered, whole blood from freshly-caught albacore (*Thunnus alalunga* Bonnaterre) were equilibrated at 5, 10, 15, 20, 25, 30 and 35 °C and at 0 and 1 % CO_2 for construction of oxygen dissociation curves. A strong Bohr effect ($-1{\cdot}17$), a negligible Root effect, and a reverse temperature effect ($\Delta H = +1{\cdot}72$ for 0 % CO_2 and $+0{\cdot}26$ for 1 % CO_2) characterized these hyperbolic (Hill's $n = 1{\cdot}1$) curves. The unusual reverse temperature effect was especially pronounced when blood was quickly warmed or cooled, simulating passage through the heat exchanging, countercurrent vascular rete system of this warm-bodied fish. A diagrammatic model of blood gas dynamics in the rete incorporating these *in vitro* data illustrates protection of arterial oxygen from premature haemoglobin dissociation and consequent loss to the venous circulation as blood warms in the rete. More conventional temperature effects on the carbon dioxide equilibria of albacore blood lower the P_{CO_2} of venous blood being cooled in the rete. This reduces the venous–arterial P_{CO_2} gradient, thereby minimizing the diffusion of CO_2 to arterial blood with resulting haemoglobin-oxygen dissociation *via* the strong Bohr effect. The temperature range (10–30 °C) over which the albacore haemoglobin-oxygen binding exhibits the reversed thermal effect closely matches the maximum thermal gradient (ambient water–core body temperature) typically present in this fish, suggesting that its highly specialized haemoglobin-oxygen dissociation characteristics evolved within – and now establishes thermal limits upon – the existing geographic distribution of this species.

INTRODUCTION

It is well established that tunas (family Scombridae) and mackerel sharks (Lamnidae) utilize countercurrent vascular retia mirabilia in conserving metabolic heat and

Key words: Haemoglobin, warm-bodied fish, albacore.

maintaining an elevated body temperature (Carey *et al*. 1971; Graham & Diener, 1978; Stevens & Neill, 1978). Although the brain and viscera are also warmed in some of these species, the highest temperatures always occur in and around the deeply positioned packs of red muscle (Carey & Teal, 1966, 1969*a*,*b*; Graham & Dickson, 1981). Retia are composed of dense bundles of arteries and veins and are situated in series with the major systemic arterial and venous circulation entering and exiting red muscle (Graham & Diener, 1978). Oxygenated blood that has just reached thermal equilibrium with ambient sea water in the gills enters the rete on the arterial side while warmed, deoxygenated, and carbon dioxide-laden blood enters on the venous end. In the rete, countercurrent flow and the high surface area contact between the two blood supplies facilitate the transfer of nearly all of the metabolic heat in the venous blood to arterial blood, thus conserving muscle temperature (Carey, 1973; Stevens & Neill, 1978; Carey, Teal & Kanwisher, 1981). After exiting the rete arterial blood continues to the red muscle capillary beds and cooled venous blood flows to the gills where carbon dioxide is excreted and oxygen is loaded.

This heat conservation system utilizes the blood as the heat transferance medium with conduction across the vessel walls of the rete. As a consequence, the blood warms and cools rapidly as it passes through the rete. However, it is known that temperature increases result in a drop in blood pH (Howell, Baumgardner, Bondi & Rahn, 1970) of approximately $-0{\cdot}012$ to $-0{\cdot}019$ pH units per °C, depending on the temperature (Reeves, 1976). Warming also decreases the solubility of oxygen and carbon dioxide in plasma. Together or separately, a temperature increase, a pH decrease, and a P_{CO_2} increase all characteristically reduce blood (haemoglobin) oxygen affinity of fish blood (see reviews by Randall, 1970; Wood & Lenfant, 1979).

Studies on blood gas equilibria in warm-bodied fish began with Rossi-Fanelli & Antonini's work (1960) on bluefin tuna (*Thunnus thynnus*) haemoglobin. They found a very small effect of temperature on oxygen affinity (apparent heat of oxygenation, $\Delta H = -1{\cdot}8\ \mathrm{kcal\,mol^{-1}}$), but performed their studies with crystalline haemoglobin in buffered solutions (Rossi-Fanelli & Antonini, 1960). Anderson, Olson & Gibson (1973) also noted small temperature effects for mako shark (*Isurus oxyrinchus*) and bigeye tuna (*Thunnus obesus*), although stripped haemoglobin haemolysate solutions were used. Graham (1973) proposed that the small temperature effects of warm-bodied fishes may have evolved to eliminate premature oxygen dissociation in the retia, but he included little data to support this hypothesis. Sharp (1975) constructed oxygen dissociation curves using erythrocytes of bigeye tuna, bluefin tuna, albacore (*Thunnus alalunga*), and yellowfin tuna (*Thunnus albacares*). However, Sharp suspended the cells in buffered glycerol solutions and many of the measurements were at higher temperatures (to 37 °C) and lower pH values (to 6·60) than are probably naturally experienced by these species. Carey & Gibson (1977) described a reverse temperature effect and crossing of oxygen dissociation curves constructed at 14 and 22 °C for bluefin tuna. However, buffered haemoglobin solutions were again used to arrive at these results. Carey & Gibson (1983) constructed oxygen dissociation curves from bluefin tuna whole blood at 5–35 °C. They found virtual temperature independence, but gave no pH data. However, they provide evidence for a reverse temperature effect with bluefin haemoglobin solutions between pH 7·0 and 8·5. Thus, a study using whole blood from freshly-caught specimens and employing appropriate pH and temperature regimes was considered to be of particular value in advancing our understanding of temperature-related haemoglobin-oxygen dynamics in warm-bodied fishes.

The main problem in studying tuna is that they range freely in habitats often at great distances from the closest laboratory having appropriate facilities and instrumentation to make the needed measurements. The first objective of the present study was to investigate the blood oxygen dissociation characteristics of albacore using fresh, unbuffered, whole blood over the range of internal and external temperatures appropriate for this species. This would include arterial and venous CO_2 tensions and the fast transitions in temperature that occur as blood traversed the rete. The second objective was to determine the thermal limits and optima for oxygen binding in albacore blood. This tested Graham's (1973) hypothesis and revealed how the albacore's blood gas transport mechanisms have evolved in response to both the range of ambient temperatures and dissolved oxygen conditions encountered by this species and to the gradient between its ambient and core body temperature which, although affected by many factors, remains primarily dependent upon fish activity.

MATERIALS AND METHODS

Albacore (body weight range = 5·720–10·325 kg) were captured by hook and line using trolled feathered jigs aboard the U.S. NOAA National Marine Fisheries Service R.V. *David Starr Jordan* during the first two of the three legs of the 1981 albacore physiology cruise. Using hydraulic fishing reels, fish were landed within 30 s of being hooked. A running seawater hose (1·2 cm i.d.) was immediately placed in the mouth of the fish as it rested upon the deck for artificial gill ventilation. Blood samples (44–94 ml) were immediately taken from the heart or a cutaneous vessel using heparinized, 20 ml polypropylene syringes and 20 gauge needles. Needles were removed and blood was immediately transferred to heparinized polypropylene vials. Clotting was negligible and blood was either used immediately or stored at 4 °C to be used within 12 h.

Aboard the research vessel, whole unbuffered albacore blood was equilibrated with gases in a pair of rotating, Hall-type glass tonometers (Hall, 1960). One tonometer had a continuous flow of humidified, deoxygenated gas (100 % N_2 or 99 % N_2 + 1 % CO_2), while the other had a continuous flow of humidified, oxygenated gas (100 % air or 99 % air + 1 % CO_2), respectively. Various mixtures of the blood from the two tonometers were taken in 1 ml glass syringes, each having a metal mixing bead, to simulate 'arterial' (0 % CO_2) and 'venous' (1 % CO_2) blood. Volumes of blood withdrawn from the tonometers, adjusted for the volume of the beads and the syringe and needle deadspaces, were selected to give 0, 20, 50, 80, 95 and 100 % oxygenated mixtures (= % saturation) after mixing in the syringe for 30 s. Oxygen tension (P_{O_2}) measurements from each mixture were made using a Radiometer PHM 71 Mk. 2e analyser and Radiometer E5046/D616 thermostatted P_{O_2} electrode assembly to construct blood oxygen dissociation curves (Edwards & Martin, 1966). In addition, pH measurements of the blood mixtures were made using a Radiometer G297/K497 thermostatted pH/reference electrode system wired to the PHM 71 Mk. 2e analyser. P_{O_2} and pH electrodes were 'two-point' calibrated with air/N_2 and an aneroid barometer to ±0·1 Torr and Harleco precision buffers to ±0·001 pH units, respectively, immediately before each mixture measurement. Mean pH values for each fish at each P_{CO_2} level were calculated by initial conversion to $[H^+]$ values (Davenport, 1974). Blood oxygen capacity (Cb_{O_2}) was determined by direct measurements of oxygen content of the 100% saturation blood using a Lexington Instruments Lex-O_2-Con Model M analyser.

Temperatures (5–35 ± 0·5 °C) were maintained in the insulated tonometer water bath by opposition of a thermostatted Lauda Model K-2/R chiller and a 500 W immersion heater wired to an adjustable thermoregulator and relay (Versatherm) with vigorous circulation by a submersible pump. For construction of constant-temperature blood oxygen dissociation curves, another submersible pump continuously circulated water from the tonometry bath through the water jackets of the P_{O_2} and pH electrodes. Blood oxygen dissociation curves resulting from a rapid 20 °C temperature increase or decrease (simulating passage through the heat exchanging rete) were made possible by moving the water jackets' pump to a second insulated water bath kept 20·0 °C cooler or warmer than the tonometer bath. For these rapid temperature change measurements, mixed blood samples from the tonometers at 10 or 30 °C were injected into the electrode measurement chambers maintained at 30 or 10 °C, respectively, for P_{O_2} and pH measurements.

Bohr effect was calculated by $\Delta \log P_{50}/\Delta pH$ and Root effect was calculated from % loss in Cb_{O_2} (Hayden, Cech & Bridges, 1975). The apparent heat of oxygenation (ΔH) was calculated using a form of the Van't Hoff equation (Wood & Lenfant, 1979). Packed cell volumes (haematocrits) were determined numerous times on blood samples from each fish to monitor changes as blood was added to tonometers for each curve and to ascertain visually the presence of significant haemolysis. Almost all of the plasma had a pale straw colour and no blood was used which had more than a very slight pink tinge in plasma colour, indicating minimal haemolysis. Blood samples from each fish were also fixed for lactic acid determinations (BMC Single Vial Lactate Kit).

Albacore blood gas equilibria measurements were continued at the Scripps Institution of Oceanography, Physiological Research Laboratory using whole blood from legs two and three of the cruise. Available instrumentation at this laboratory allowed us to measure blood CO_2 tensions (Radiometer PHM71 Mk. 2e analyser with E5036 electrode) and CO_2 concentrations (Capni-Con, Cameron Scientific Instruments, Port Aransas, Texas) on blood mixtures from the same tonometers in addition to the other measurements made at sea. In addition, whole blood CO_2 dissociation curves were constructed at 10 and 30 °C from the blood of one albacore in similar fashion to the blood oxygen dissociation curves described above. In this case, however, blood was equilibrated with N_2 and CO_2 in the paired tonometers. ($P_{O_2} =$ 0 Torr, 1 Torr = 133·322 Pa). Blood P_{CO_2} and pH was measured with the Radiometer systems and CO_2 contents of each mixture were measured with the Capni-Con. Plasma CO_2 contents were calculated using the Henderson-Hasselbalch equation (Davenport, 1974) with constants published by Reeves (1976). These laboratory determinations were made on blood within 24 h post-sampling, except for the CO_2 dissociation curves which were made 3 days post-sampling. However, the blood was stored at 4 °C in polypropylene syringes or vials having large air spaces for the metabolic oxygen requirements of these aerobic, nucleated erythrocytes (Eddy, 1977). The air in these containers was renewed and gently mixed with the blood every 4–12 h.

RESULTS

The morphological and physiological characteristics of the five shipboard-sampled albacore are shown in Table 1. Generally the blood oxygen dissociation curves of albacore were quite consistent among fish tested, hyperbolic in shape, and unusually affected by temperature. Curves at 25 °C and 0 % CO_2 were constructed for all five albacore sampled at sea and showed a mean ± S.D. (range) of 8·3 ± 1·5 (6·5–9·9) Torr for the P_{50}, 26·6 ± 2·5 (23·3–29·0) Torr for the P_{80} and 56·7 ± 5·6 (53·7–65·0) Torr for the P_{95}. The variation in P_{50} seemed to stem primarily from small differences in blood pH measured for individual fish (Table 1). The curves were strongly hyperbolic with a Hill's coefficient (Wyman, 1948) of 1·11 and showed a *reverse* temperature effect (Fig. 1). In contrast to almost all haemoglobins previously studied, oxygen affinity *increases* with increasing temperature (Figs 1–3). The overall calculated apparent heat of oxygenation (ΔH) was +1·72 for 0 % CO_2 and +0·26 for 1 % CO_2.

A temperature increase accentuated the reverse temperature effect. Whereas the mean P_{95} of 'arterial' blood (0 % CO_2) was 93·3 Torr at 10 °C and 47·0 Torr at 30 °C, it was only 36·3 Torr when rapidly heated from 10 to 30 °C (Fig. 3).

In contrast to the atypical temperature effects on the albacore haemoglobin(s), the pH/CO_2 effects were more conventional. The mean Bohr effect for all shipboard data (10–35 °C) was −1·17. Using only P_{50} and pH data measured from the same fish at both CO_2 tensions, the mean Bohr effect was −1·31 (25–35 °C). A small mean Root effect of −4 % was calculated for all shipboard albacore over 10–35 °C. A small gain (+5 %) in mean Cb_{O_2} was calculated for the fish in which Cb_{O_2} was measured at both P_{CO_2} levels over 25–35 °C.

To visualize the blood gas dynamics across the heat exchanger, a diagrammatic model has been fitted with available *in vitro* data (Fig. 4). Because of the lack of *in vivo* blood gas data on settled-down fish, 'arterial' blood is assumed to be at 95 %

Table 1. *Morphological and physiological characteristics of shipboard-sampled albacore*

Fish No.	Fork length (cm)	Live weight (kg)	Blood P_{50} at 25 °C and 0 % CO_2 (Torr)	x̄ Haematocrit (%)	Blood oxygen capacity at 25 °C and 0 % CO_2 (ml dl^{-1})	x̄ Blood pH at 25 °C and 0 % CO_2	Blood lactic acid concentration (mg dl^{-1})
1	77·5	8·333	9·8	56·9	22·9	7·68	57·67
2	66·5	5·720	6·5	47·7	19·0	7·61	46·88
3	78·5	9·250	8·1	52·6	22·1	7·76	57·80
4	76·0	8·630	7·1	56·1	22·6	7·66	44·37
5	82·5	10·325	9·9	51·5	22·6	7·76	43·88
x̄	76·2	8·450	8·3	53·0	21·8	7·69	50·12
S.D.	5·9	1·705	1·5	3·7	1·6	0·06	7·04

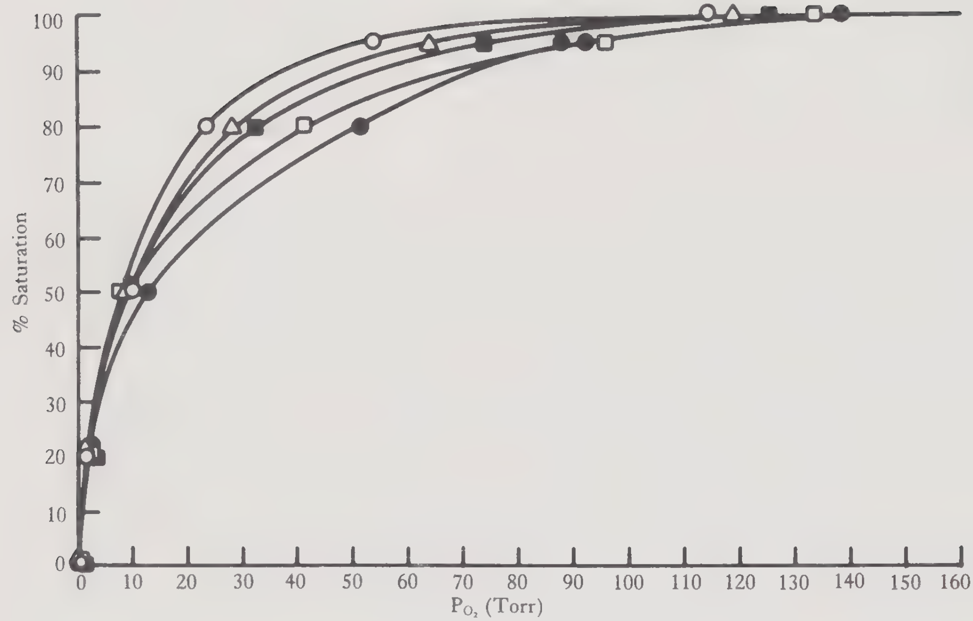

Fig. 1. Whole blood oxygen dissociation curves from albacore (*Thunnus alalunga*) no. 1, equilibrated at 0 % CO_2 and 5 °C (●), 10 °C (□), 15 °C (■), 20 °C (△) and 25 °C (○).

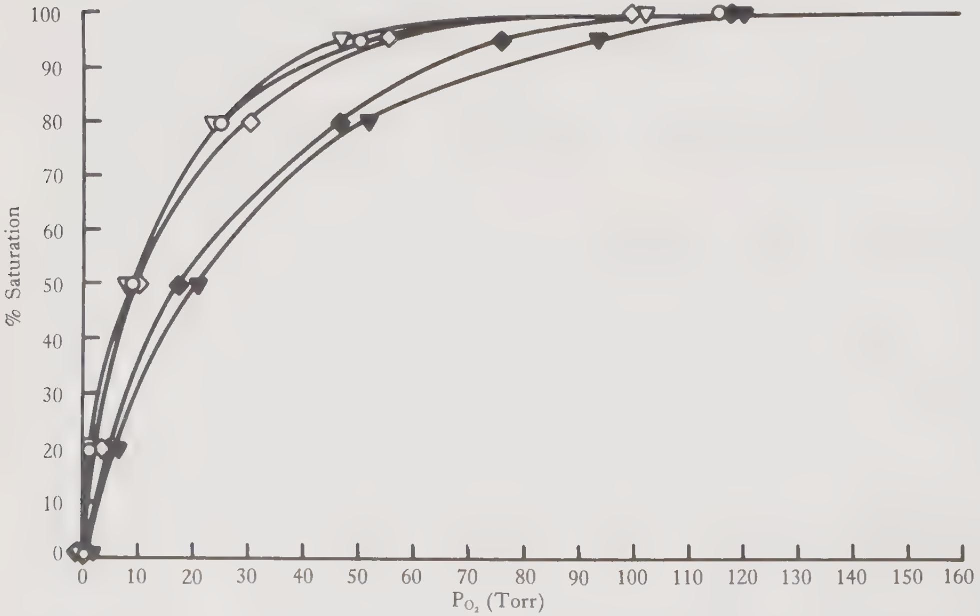

Fig. 2. Whole blood oxygen dissociation curves from albacore (*Thunnus alalunga*) no. 3, equilibrated at 0 % CO_2 and 25 °C (○), 30 °C (▽), and 35 °C (◇) and at 1 % CO_2 and 30 °C (▼) and 35 °C (◆).

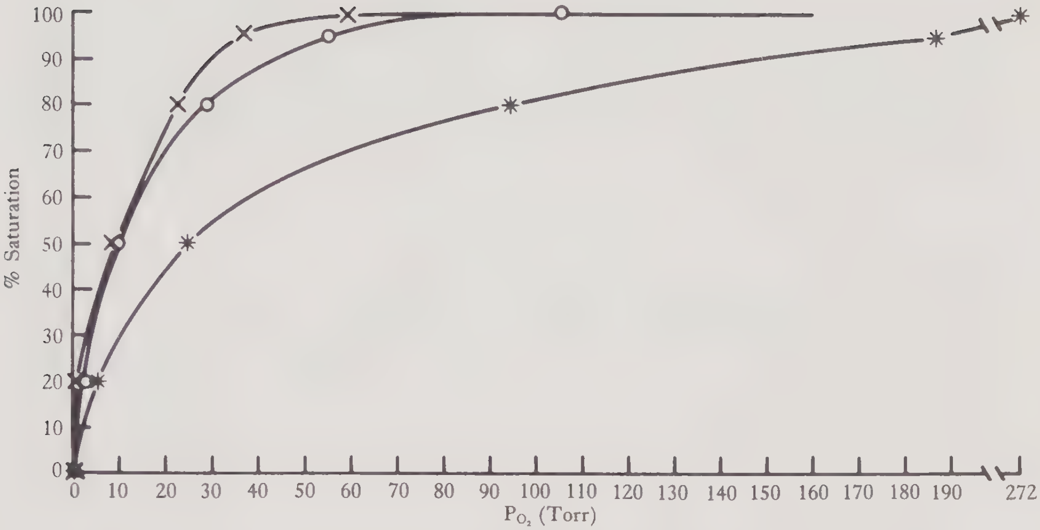

Fig. 3. Whole blood oxygen dissociation curves from albacore (*Thunnus alalunga*) no. 5, equilibrated at 0 % CO_2 and 25 °C (○), and at 10 °C and then quickly warmed to 30 °C (×), and at 1 % CO_2 and 30 °C and then quickly cooled to 10 °C (∗).

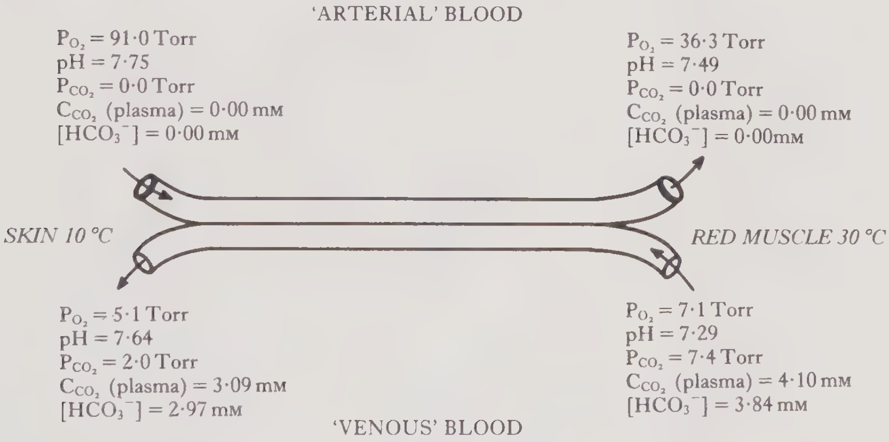
'ARTERIAL' BLOOD
P_{O_2} = 91·0 Torr
pH = 7·75
P_{CO_2} = 0·0 Torr
C_{CO_2} (plasma) = 0·00 mM
$[HCO_3^-]$ = 0·00 mM
P_{O_2} = 36·3 Torr
pH = 7·49
P_{CO_2} = 0·0 Torr
C_{CO_2} (plasma) = 0·00 mM
$[HCO_3^-]$ = 0·00mM
SKIN 10 °C
RED MUSCLE 30 °C
P_{O_2} = 5·1 Torr
pH = 7·64
P_{CO_2} = 2·0 Torr
C_{CO_2} (plasma) = 3·09 mM
$[HCO_3^-]$ = 2·97 mM
P_{O_2} = 7·1 Torr
pH = 7·29
P_{CO_2} = 7·4 Torr
C_{CO_2} (plasma) = 4·10 mM
$[HCO_3^-]$ = 3·84 mM
'VENOUS' BLOOD

Fig. 4. Diagrammatic model of blood gas changes occurring along a single artery (upper) and adjacent vein (lower) within a heat exchanging rete in albacore (*Thunnus alalunga*) using appropriate *in vitro* data from blood oxygen dissociation curves (see text).

saturation with respect to air and at 0 Torr P_{CO_2}. Similarly, the 'venous' blood is assumed to be at 20 % saturation and 7·6 Torr P_{CO_2}. To examine the near-maximal effects of warming (Sharp & Vlymen, 1978; Graham & Dickson, 1981) a 20 °C temperature gradient was assumed with the cutaneous vessel blood at 10 °C and the red muscular blood at 30 °C. For blood flowing into the rete at each end, *in vitro* data for albacore blood equilibrated at its respective temperature was used, while the appropriate fast temperature change data was used for outflowing blood.

Notable characteristics of this model include the inverse relationships of pH with P_{CO_2} and with temperature (Fig. 4). Blood pH decreases with increasing P_{CO_2} because of the resulting shift in the bicarbonate buffer equilibrium which dissociates more carbonic acid into hydrogen and bicarbonate ions (Albers, 1970). The relationship between temperature (T) and albacore blood pH is represented by the least-squares equations:

$$\widehat{\mathrm{pH}} = 8{\cdot}08 - 0{\cdot}016\mathrm{T}$$
$$\widehat{\mathrm{pH}} = 7{\cdot}78 - 0{\cdot}016\mathrm{T}$$

for 0 Torr P_{CO_2} and 7·6 Torr P_{CO_2}, respectively (Fig. 5).

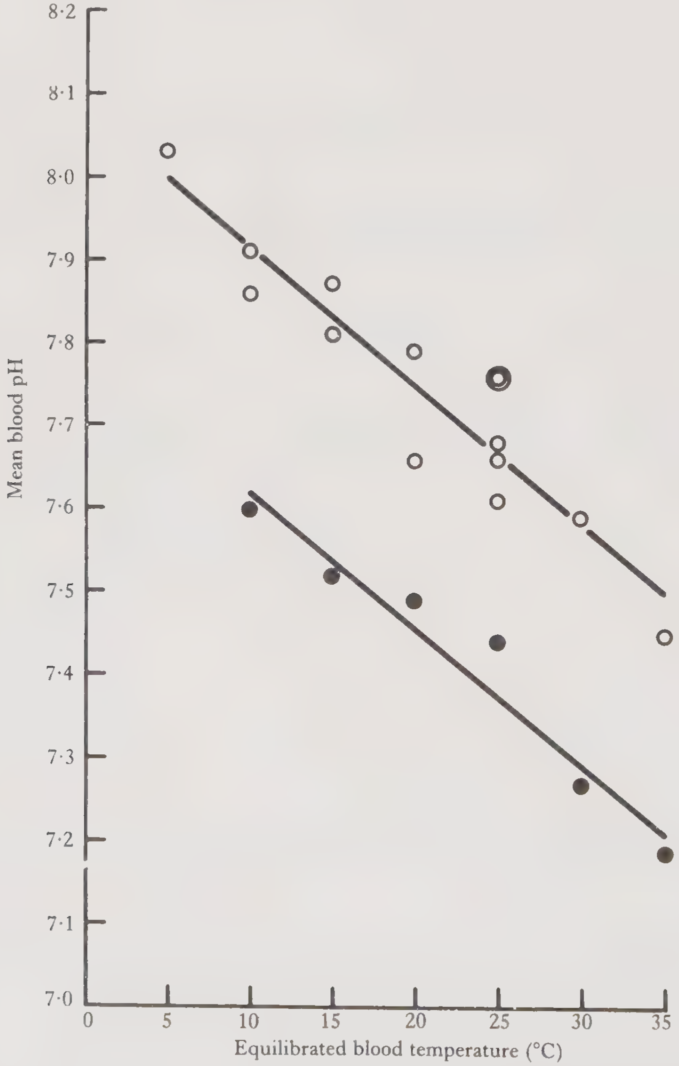

Fig. 5. Mean, unbuffered whole blood pH values of albacore (*Thunnus alalunga*) as a function of equilibrium temperature. Blood equilibrated with 1 % CO_2 (●); blood equilibrated with 0 % CO_2 (○). Heavy circle shows two identical data points.

The diagrammatic model gives insight into the importance of the reverse temperature effect. The P_{O_2} of arterial blood, declines as the blood warms in the rete, a function of the greater haemoglobin oxygen affinity at 30 °C (Figs 2, 3). Thus, rather than a temperature-induced premature oxygen dissociation in the rete the albacore haemoglobin(s) actually increases its oxygen binding, reducing the P_{O_2} gradient between 'arterial' and 'venous' blood and limiting oxygen diffusion from arterial to venous blood along the length of the retial vessels. On the venous side of the rete, P_{O_2} stays approximately constant with cooling because the reverse temperature effect is much reduced at the lower percent saturation (Figs 1–3). However, the P_{CO_2} is considerably reduced with cooling in the rete because the albacore carbon dioxide dissociation curves show a greater CO_2 affinity (i.e. more carbaminohaemoglobin) with cooling (Fig. 6). The resulting lower P_{CO_2} gradient would reduce CO_2 diffusion from venous to arterial blood and prevent premature oxygen dissociation in the rete by the Bohr effect. The calculated CO_2 content in the plasma and bicarbonate ion concentration change little with cooling (Fig. 4).

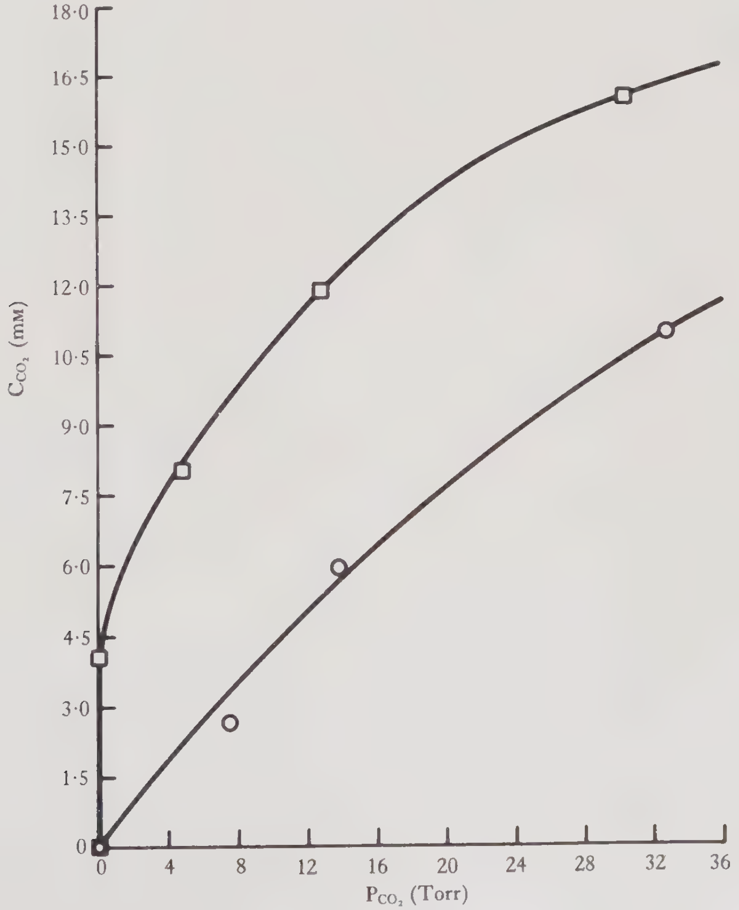

Fig. 6. Whole blood carbon dioxide dissociation curves of albacore (*Thunnus alalunga*) equilibrated at 0 % O_2 and 10 °C (□) and 30 °C (○).

DISCUSSION

In general, these albacore data reflect the high blood oxygen capacity (Table 1) and unique temperature characteristics one might expect in a highly aerobic, fast swimming, and warm-bodied tuna (Graham & Laurs, 1982). Haematocrit values closely matched the previous measurements of Alexander, Laurs, McIntosh & Russell (1980) and blood pH levels (Table 1) were in the predicted range of the curves of Howell *et al.* (1970). The most striking finding in the present study concerns the reverse temperature effect of albacore haemoglobin-oxygen binding in fresh, whole blood samples. This effect is especially dramatic with fast temperature changes. Sharp (1975) previously described a hyperbolic oxygen dissociation curve for albacore blood but failed to find the reverse temperature phenomenon, probably because of the high temperatures (25 and 37 °C) he used. Data from the present study show that the reverse temperature effect is diminished and 'reverts' to the more typical form between 30 and 35 °C. Collett & O'Gower (1972) described a reverse temperature effect in buffered haemolysate haemoglobin solutions from three species of arcid clams. Normal, decreased oxygen affinities were displayed by these haemoglobins with increasing temperatures up to 20–25 °C, but affinities increased at higher temperatures. Collett & O'Gower attributed this phenomenon to part of these species' physiological adaptations to intermittent respiratory stress in warm, marine environments. Carey & Gibson (1977, 1983) imply an increased respiratory efficiency in the bluefin tuna heat exchanger because there is a reverse temperature effect. Since the reverse temperature phenomena described by Collett & O'Gower (1972) and by Carey & Gibson (1977, 1983) both arose from experiments using haemoglobin solutions, we conclude that this effect has a haemoglobin molecular basis in the present study with albacore whole blood.

Potential experimental drawbacks of our study merit comment. One concerning our fast temperature change blood gas values concerns the time course of the temperature change. Injection of blood mixtures equilibrated at one temperature into an electrode sample chamber thermostatted at the second temperature probably does not exactly mimic the changes in blood temperature that takes place in the seconds required for blood to traverse the rete *in vivo*. Moreover, at 30 and 10 °C, it takes approximately 1·5 and 3·5 min, respectively, for the P_{O_2} electrode and meter to come to a stable reading. As *in vivo*, oxygen cannot escape from the electrode chamber and thus the 'instantaneous' P_{O_2} values may actually be more extreme, i.e. lower with quick warming and higher with quick cooling, based on comparisons with temperature-equilibrated curves (Figs 1–3). This seems particularly likely in view of the respiration of these nucleated red blood cells which would deplete oxygen during the time needed to obtain stable readings. The especially prolonged time course of the 30 to 10 °C switch would actually have a minimal effect on the functional relationships shown in the diagrammatic model (Fig. 4) due to the vastly reduced reverse temperature effects at 20 % saturation (Figs 1–3).

Assumptions concerning the model also deserve comment. A 20 °C temperature shift across the rete is probably maximal (Sharp & Vlymen, 1978; Graham & Dickson, 1981), and this large shift was desired to elucidate the relevant blood gas dynamics. Graham & Dickson (1981) measured red muscle temperatures between 28 and 29 °C in an exercising albacore situated in water at 13 °C in a shipboard tank. Laurs, Dotson, Dizon & Jemison (1980) found that acoustically-tagged albacore remained in water between 9 and 14 °C. Also, the 10–30 °C range lies wholly within and roughly defines the thermal zone of the reverse temperature effect (Figs 1, 2). Blood entering the white muscle would obviously be warmed less than that entering the red muscle through the rete (Graham & Dickson, 1981). Also, a 20 °C gradient between the ambient water and the entire red muscle mass would not be expected at all times. P_{O_2} and pH conditions during a <20 °C temperature shift could be crudely estimated from the curves shown in Figs 1, 2 and 5. The percent saturation (95 % for 'arterial' and 20 % for 'venous') and P_{CO_2} levels (0 Torr for 'arterial' and 7·6 Torr for 'venous') seem reasonable for fish of high routine activity levels (Root, 1931; Stevens & Randall, 1967; Cameron, 1971; Holeton, Pawson & Shelton, 1982).

It is logical that the fast temperature change data be used for both the arterial and venous blood flowing from the rete due to the probable short residence time of blood in this structure. It also seems reasonable that 10 °C equilibrium data be used to model the arterial flow. Free-swimming albacore occur in water of this temperature (Laurs *et al.* 1980). Also, arterial blood reaches thermal equilibrium with ambient water in the gills and does not gain heat *en route* to the rete (Carey *et al.* 1971; Stevens & Neill, 1978). On the venous side, all regions in the red muscle would not be expected to be at 30 °C, although this temperature may reflect the average (Graham & Dickson, 1981). Thus, most CO_2 would be added to venous blood at about 30 °C (Fig. 4).

Assuming, then, that the diagrammatic model gives us a reasonable idea of the *in vivo* retial blood gas dynamics, what does this mean to the albacore? On the arterial side, it means that more oxygen is bound by haemoglobin rather than released prematurely in the rete. The greater haemoglobin-oxygen affinity has two favourable aspects. The first is that the plasma P_{O_2} is lowered in the arteries, which lowers the arterio-venous P_{O_2} gradient and minimizes the diffusion potential for oxygen to the venous blood, ensuring that it reaches the muscle capillaries. The second is that some of the oxygen is removed from the plasma, thereby opening some solubility 'space' for the inert gases (principally, nitrogen) to stay dissolved. Using gas solubility table (Weiss, 1970) calculations, a 1 % salt solution (simulating plasma) that is 95 % air-saturated at 10 °C will increase in total gas saturation to 140 % (1·4 atm = 141 855 Pa) when heated to 30 °C. The P_{O_2} reduction in albacore blood concomitant with this warming would limit this total gas saturation to 119 %. Using the reasoning of Kiesow (1974), this excess P_{N_2} may be the mechanism for the higher oxygen affinity of the haemoglobin upon rapid warming. However, human erythrocytes and 50–100 atm P_{N_2} were utilized in Kiesow's study. Obviously, nitrogen gas bubbles would severely impair capillary circulation (Hochachka & Somero, 1973). Although a total gas saturation of 119 % is capable of supporting bubble formation (Bouck, 1980), a combination of hydrostatic (depth) and blood pressure may satisfactorily ameliorate this condition (Bouck, 1980). Indeed, the prevention of gas bubble formation in the blood may be one limitation on the maximum temperature differential across the rete.

On the venous side, the P_{CO_2} is reduced with cooling, decreasing the P_{CO_2} arterio-venous gradient and thereby minimizing the potential for CO_2 diffusion into retial arteries. The strong Bohr shift calculated for albacore indicates that oxygen would dissociate from the haemoglobin in the rete if significant quantities of CO_2 were introduced into the arteries. The albacore Bohr effect ($-1{\cdot}17$ overall) compares with the continually active, but not warm-bodied Atlantic mackerel, *Scomber scombrus* at $-1{\cdot}2$ (Hall & McCutcheon, 1938). Both of these display more dramatic Bohr effects than rainbow trout, *Salmo gairdneri* at $-0{\cdot}57$ (Eddy, 1971). The small Root shift of albacore befits a species with a relatively small swimbladder (Riggs, 1970)

Blood lactic acid concentrations of the albacore were not high when compared with other species. For example Holeton *et al.* (1982) measured mean lactate concentrations of $>80\,\mathrm{mg\,dl^{-1}}$ in feather-jig-caught Atlantic mackerel. Also, Soivio, Nikinmaa, Nyholm & Westman (1981) measured mean lactate concentrations approximating $68\,\mathrm{mg\,dl^{-1}}$ (arterial) and $81\,\mathrm{mg\,dl^{-1}}$ (venous) in resting rainbow trout. The lack of a significant correlation ($r = 0{\cdot}25$, $P >> 0{\cdot}05$) between albacore blood lactate concentrations and mean blood pH, measured at the same temperature and P_{CO_2} conditions, also indicates a minimal effect of lactate on blood gas relationships in the present study (Table 1).

This study reveals that temperature has a reversed effect on the haemoglobin-oxygen dynamics of albacore blood. Our analysis of this effect in relation to the structure and function of a heat-exchanging rete suggests that it is an adaptation which enables the albacore to optimize the physiological consequences of rapid changes in blood temperature for red muscle respiratory gas transport. The close correspondence between the optimal thermal range (10–30 °C) for the reversed effect and the typical gradient present between ambient (sea water) and core (red muscle) temperatures for albacore is noteworthy and additionally suggests that the oxygen transport mechanism of this species has become, through natural selection, precisely poised to operate between environmental and deep body temperatures for the purpose of sustaining aerobic muscle metabolism. This further implies that geographical (by temperature) distribution limits of albacore may in turn be set by its thermal optimum for oxygen transport. Of course, even within its normal zoogeographic range, an albacore's water–red muscle thermal gradient is not constant and could become altered either by changes in red muscle metabolism (i.e. swimming velocity), shifts in ambient temperature, or both (Graham & Dickson, 1981). However, a large sustained shift in the gradient seems unlikely. This is because albacore swimming in nature spend most of their time in a narrow range of temperatures (9–12 °C, Laurs *et al.* 1980) and the scope for metabolic heat production by albacore red muscle is constrained within limits. These limits are set at the low end by the minimum swimming velocity needed for an albacore to maintain hydrostatic equilibrium (Dotson, 1976; Magnuson, 1978), and at the high end by the capacity of the cardiovascular system to sustain aerobic metabolism (heat production) in active red muscle (Graham, 1983). On the other hand albacore migrating into the eastern Pacific Ocean may encounter layers of 9–12 °C water in which the oxygen tensions reflect 60 % air saturation (Laurs & Lynn, 1977) which would reduce haemoglobin saturation to some extent (Figs 1–3). If this requires an albacore to change depth to shallower (warmer), more oxygenated water an acclimatory shift may occur in its optimal thermal gradient for oxygen transport. Alternatively this species could compensate for a decreased ambient oxygen supply by increasing its blood oxygen affinity.

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Guidelines for Reducing Porpoise Mortality in Tuna Purse Seining

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ABSTRACT

More than a decade has passed since the passage of the Marine Mammal Protection Act of 1972. During that time the U.S. tuna purse seine fleet reduced its incidental porpoise mortality rate more than 10-fold. This was made possible through the development of gear and techniques aimed at reducing the frequency of many low probability events that contribute to the kill.

Porpoise are killed by becoming entangled or entrapped in folds and canopies of the net and suffocating. The configuration of the net, both before and during the backdown release procedure, is a major determinant of the number of porpoise killed. Speedboats can be used to tow on the corkline to prevent net collapse and also to adjust the net configuration to reduce net canopies prior to backdown. Deepening a net can reduce the probability of porpoise being killed by prebackdown net collapse. The effects of environmental conditions and mechanical failures on net configuration can result in high porpoise mortality unless mitigated by skilled vessel maneuvers or prevented by the timely use of speedboats to adjust the net.

The backdown procedure is the only means to effectively release captured porpoise from a purse seine. It is also the time during the set when most of the mortality occurs. The use of small mesh safety panels and aprons in the backdown areas of nets reduces porpoise entanglement, and increases the probability of an effective release. The tie-down points on the net for preparing the backdown channel must be properly located in order to optimize porpoise release. A formula uses the stretched depth of the net to calculate one of these points, making it a simple matter to locate the other. Understanding the dynamics of the backdown procedure permits a thorough troubleshooting of performance, thus preventing the repetition of poorly executed backdowns and thereby reducing mortality.

Porpoise that cannot be released must be rescued by hand. A rescuer in a rigidly inflated raft can rescue porpoise effectively at any time during a net set. Hand rescue can make the difference between above average kill and zero kill sets. In all circumstances, the skill and motivation of the captain and his crew are the final determinants in the prevention of incidental porpoise mortality in tuna seining.

INTRODUCTION

The purse seining method of catching yellowfin tuna, *Thunnus albacares*, in association with schools of porpoise[4] in the eastern tropical Pacific has been described by Perrin (1969) and Peters (1979). The primary target species, in order of importance, are the spotted dolphin, *Stenella attenuata*, and the spinner dolphin, *S. longirostris*, with occasional net sets made on schools of the common dolphin, *Delphinus delphis*. Schools of these porpoise, ranging in size from 50 to several thousand, are herded with speedboats and encircled with a purse seine net that is from 900 to 1,400 m long and as much as 130 m deep. After the porpoise are encircled, the bottom of the net is pursed, entrapping the mammals and any tuna that are associated with the school.

The incidental mortality rate of these marine mammals was estimated to exceed 40/set[5] in 1972, the year the Marine Mammal Protection Act was passed (Table 1, Fig. 1). The U.S. tuna fleet, with assistance from both private and government fishery specialists, succeeded in reducing their kill rate to 4/set by 1980. During this period the development and utilization of new gear and procedures, coupled with increased operator skill, reduced the frequency of high kill sets (Table 1) and increased the number of zero-kill sets (Fig. 2). The technology leading to these results is in varied used in both the domestic and foreign tuna fleets.

Individual captains have repeatedly demonstrated that over 99.9% of all captured porpoise can be released unharmed when the gear and techniques described in this report are skillfully employed. In the absence of future innovations to reduce mortality, further improvements in fleet performance may only be gained by heightening the skill and motivation levels of the vessel operators and by improving the durability and reliability of vessel equipment. This is no easy task. Vessel operators must be constantly prepared to prevent, avoid, or remedy a collection of very low probability events, any one of which may result in porpoise being killed. They must attempt to minimize the negative affects of environmental conditions, equipment failures, and porpoise behavior on the outcome of each set. This diligence must be maintained in the face of the risk of losing part or all of the tuna catch

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[4] Porpoise, in this paper, is used as a general term referring collectively to all small cetaceans impacted by the fishery. While dolphin is the more scientifically correct term, porpoise continues to be the term used by fishermen and researchers alike. The three major species involved are the spotted, spinner, and common dolphins: *Stenella attenuata*, *S. longirostris*, and *Delphinus delphis*.

[5] Mortality or kill refers to porpoise mortality incidental to the catch of yellowfin tuna, *Thunnus albacares*. The "set" is defined as a single deployment of a purse seine net around an aggregation of porpoise and/or tuna. Tuna catches are expressed in short tons.

Table 1.—Summary statistics of porpoise sets from NMFS observer trips, 1971-80. Numbers in parentheses are sample sizes.

Statistic	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
Total no. porpoise sets	51	273	705	993	948	754	3,408	1,811	2,036	1,007
No. pure spotted porpoise sets	23	117	302	425	361	255	1,093	931	1,015	587
No. pure spinner porpoise sets	0	0	17	15	11	9	14	8	7	6
No. mixed spotted and spinner sets	25	132	279	365	412	399	756	680	503	257
No. common-dolphin sets	2	23	105	142	96	55	10	4	7	1
No. others and unidentified porpoise sets	1	1	2	46	68	36	1,535	188	504	156
Average tons of yellowfin/set	18(48)	20(272)	14(705)	11(993)	13(948)	13(754)	12(3,408)	11(1,811)	11(2,035)	10(1,006)
Average number of porpoise caught/set	219(48)	486(245)	378(705)	355(980)	634(947)	816(720)	813(3,107)	821(1,612)	658(1,797)	643(905)
Average porpoise school size/set[1]	298(48)	1,007(239)	907(703)	1,163(866)	1,216(945)	1,419(734)	1,656(3,205)	1,446(1,669)	1,170(1,870)	1,054(935)
Average porpoise kill/set	70(48)	43(272)	19(705)	12(993)	16(947)	14(754)	3(3,408)	4(1,809)	3(2,034)	4(1,006)
Average porpoise kill/ton of yellowfin	3.8	2.2	1.3	1.1	1.3	1.1(754)	0.2(3,408)	0.4(1,809)	0.2(2,033)	0.3(1,006)
Percent porpoise killed of porpoise caught	31.9	8.9	4.9	3.4	2.5	1.8(720)	0.4(3,107)	0.5(1,611)	0.3(1,797)	1.6(904)
Percent of school captured[1]	73.5	48.3	41.7	30.5	52.2	57.4(719)	49.6(2,984)	57.5(1,540)	58.3(1,730)	63.1(885)
Percent of school killed[1]	23.5	4.3	2.1	1.0	1.3	1.0(734)	0.2(3,205)	0.3(1,667)	0.2(1,868)	0.4(934)
Percent of sets catching yellowfin	92(48)	89(273)	82(705)	74(993)	82(948)	83.3(754)	84.7(3,408)	85.3(1,811)	87.3(2,035)	91.3(1,006)
Percent of sets catching porpoise	100(48)	91(273)	86(705)	83(993)	91(947)	91.4(720)	95.5(3,107)	97.4(1,612)	97.2(1,797)	99.3(905)
Percent of sets catching porpoise with 0 killed	2(48)	12(248)	18(601)	22(827)	24(863)	30.4(658)	56.5(2,968)	58.4(1,569)	71.4(1,746)	67.5(898)

[1]Estimates generally have a low precision.

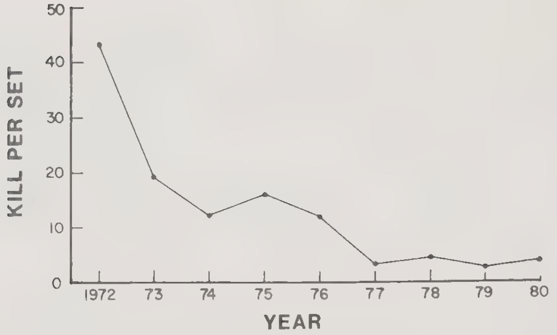

Figure 1.—Average porpoise kill per observed set.

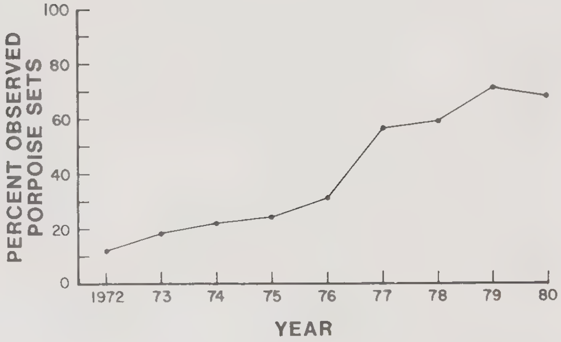

Figure 2.—Percent of observed porpoise sets with zero porpoise killed.

while attempting to release every captured porpoise. The annual kill quotas for the U.S. fleet are set at 20,500 animals/yr (NOAA 1980[6]) for 1981 through 1985. At this level, the performance of individual vessels can have a major impact on the length of the fishing season, justifying extreme diligence by vessel operators.

The intent of this paper is to bring together information relevant to the occurrence and prevention of porpoise mortality in tuna purse seining as a record of the present state of the art and as a baseline for future research and development. It should be noted that there are many events which may increase the probability of porpoise being killed for which no specific preventive or remedial measures exist. The most important of these are discussed.

Porpoise are killed when confined by the net in such a way that they are unable to rise to the surface to breathe. Aside from occasional shark attacks and encounters with vessel power equipment (speedboats, power block, net skiff, brailer, etc.), death by suffocation is the rule. Physically, the animals are either entangled individually in the meshes or are entrapped singly or in groups by folds or "canopies" of webbing. The probability that animals will become entangled or entrapped depends upon the configuration of the net, the number of porpoise and amount of tuna captured, their behavior, and the skill of the vessel operator. Table 2 shows the

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[6]NOAA. 1980. Draft Environmental Impact Statement: Proposed regulations and conditions for the issuance of a general permit governing the taking of marine mammals associated with tuna purse seining operations. Department of Commerce, National Oceanic and Atmospheric Administration, NMFS, November 1980, 88 p.

Table 2.—Numbers of porpoise killed by general cause in sets with greater than 15 porpoise killed; NMFS observed trips 1977-80.

Year	Number of sets (%)	Total kill (%)	Backdown canopies				Prebackdown net collapse	Backdown channel collapse	Malfunction mortalities	All other causes	Unknown
			Bow	Stern	Other	Total					
1977	135 (4.0)	5,277 (51.6)	749	1,539	774	3,062	440	346	329	339	780
1978	73 (4.6)	4,932 (68.0)	478	486	872	1,836	1,897	338	397	243	221
1979	54 (3.5)	2,879 (47.1)	960	173	43	1,176	284	326	84	925	84
1980	30 (2.9)	2,647 (65.7)	106	206	220	532	29	1,504	303	140	139
Total	292 (3.9)	15,735 (67.0)	2,293	2,404	1,909	6,606	2,650	2,514	1,113	1,647	1,224
Percent of total kill		100	15	15	12	42	17	16	7	10	8

primary causes of kill for observed sets with 16 or more porpoise killed ("disaster sets") for 1977 through 1980. Note that the primary causes are related to net configuration (i.e., backdown canopies, prebackdown net collapse, backdown channel collapse, etc.). Most of the malfunction-related kill is also due to resultant net-configuration problems. An example of an "other" cause of mortality is when the dolphins are "sacked-up" in the net with the tuna and suffocated. The unknown causes of kill are usually unobserved but are probably related to the behavior of the captured porpoise, e.g., for no apparent reason some animals dive under the boat and become entrapped in the net when trying to return to the surface.

Prevention of incidental porpoise mortality involves three distinct activities during the set: 1) From the time of encirclement until its release, the porpoise school must be safely maintained within the net, 2) the school must be released from the net without allowing the tuna to escape and, 3) individual porpoise must be rescued whenever possible.

PREVENTION OF PRERELEASE MORTALITY

The captain must safely maintain the captured porpoise in the net until he is able to release them using the backdown maneuver (Coe and Sousa 1972), normally a period of about 1 h.

Table 2 indicates that a less-than-optimum net configuration is a primary cause of porpoise mortality. Chief among the various configuration problems is prebackdown net collapse, which can be caused by strong currents, changes in wind direction and strength, major equipment malfunctions, failure of the captain to orient the set properly with the wind, or any combination of these. Regardless of the cause of prebackdown net collapse, the outcome is the same, i.e., a substantial portion of the captured porpoise school may be killed and the tuna may be lost as well. Realizing that the harvest of tuna will always involve occasional sets under adverse environmental conditions and that equipment malfunctions cannot always be prevented, the main technique for preventing prerelease mortality addresses the symptoms of net collapse rather than its causes.

Towing with Speedboats to Prevent Net Collapse

Use of speedboats can prevent or delay net collapse during pursing and hauling operations (Everett et al. 1976[7]). Net collapse occurs when the surface area of the net is decreased, forcing the porpoise into contact with the webbing and preventing them from surfacing to breathe. The effectiveness of speedboats in preventing net collapse is totally dependent on acting before the net has collapsed around a school of porpoise. The captain conducting the fishing operations must understand that once a net is collapsed, speedboats will not be able to reopen it.

Four effective methods have been demonstrated for towing on the net; each adapted to a particular set of circumstances. The four methods (Fig. 3) are: 1) Towing directly on the corkline, 2) towing on the end of one bunchline, 3) towing on the middle of an open-ended bunchline and, 4) towing on the ends of two adjacent bunchlines (one reversible and one regular which together create a towing point).

Towing directly on the corkline is best used to clear small collapsed sections or small canopies in which the corkline is tight. This method (Method 1) is particularly useful for eliminating a partially collapsed backdown channel just prior to backdown. The best towing method when the corkline is not under tension is to tow on the bunchlines so the excess slack in the corkline is gathered together into bunches (Fig. 4). Here the speedboat is hooked-up to the ends of two adjacent bunchlines (Method 4), one regular and one reversible, which together create a single towing point specifically designed for this purpose. Since the net takes many different shapes while it is pursed and/or collapsed, it may not always be possible for the speedboat to pull on the towing points. In this case the fish captain may require the speedboat to

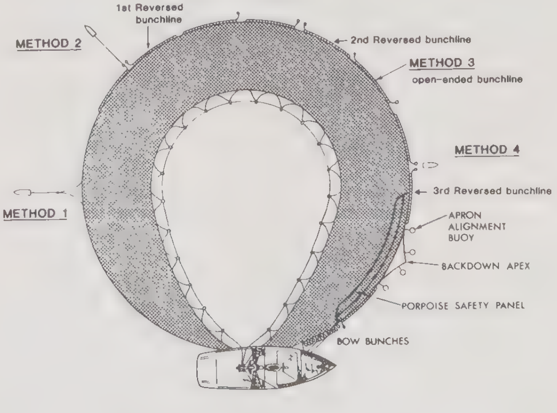

Figure 3.—Purse seine towing points for holding net open using speedboats. The three reversed bunchlines should be strategically located around the perimeter of the net but should not interfere with the porpoise apron (Method 4). Speedboats may at times find it better to pull only one regular bunchline from its end (Method 2), or from its center if its open-ended (Method 3). Speedboats may also pull directly on the corkline (Method 1) to remove small net collapses and canopies.

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[7] Everett, J., J. E. Powers, R. McNeely, J. M. Coe, and R. Butler. 1976. The use of speedboats in reducing incidental porpoise mortality in tuna purse seining. Southwest Fisheries Center Admin. Rep. LJ-76-35, 29 p.

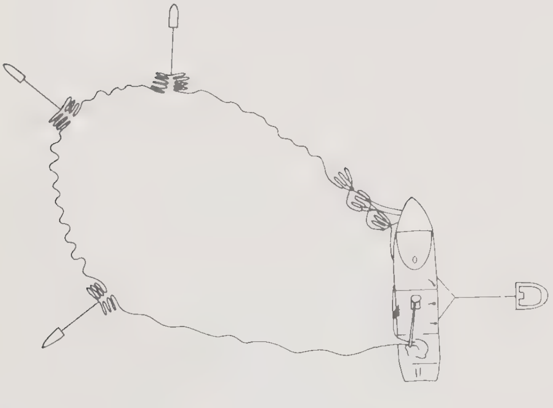

Figure 4.—Idealized configuration of net under tow by speedboats.

tow on the middle (Method 3) or the end of a single bunchline (Method 2). Whenever the corkline is slack, towing must be accomplished by towing on the bunchlines at some point which will allow the corkline to be gathered together.

Towing bridles are required on the stern of all speedboats for pulling (towing) on the net when the speedboat is engaged in the forward mode (Fig. 5). The stern towing bridle is made to hang loosely (but not so that it interferes with the propeller) and has a sliding ring for hooking-up with the towline. The towline should either be permanently attached to the sliding ring, or be made to hook-up to the ring easily with a snap hook. The opposite end of the towline should have a snap hook for quick attachment to the ends of the bunchlines or to the corkline.

Webbing shoaling near the surface may prevent a speedboat from towing with the stern towing bridle. In these circumstances the only alternative is to use the speedboat's bowline and tow in the reverse mode. This method is not nearly as efficient as towing with the stern towline, but it is useful under certain circumstances (such as small canopy removal).

Three towing points should be located on the corkline at approximately 1/4, 1/2, and 3/4 net. Each towing point is made of two adjacent bunchlines, one reversed and one normally oriented (Fig. 3). The length of these towing point bunchlines should be about 30-55 m (20-30 fathoms) for each line. These bunchlines should be positioned so that their use will not interfere with formation of the backdown channel. Use of a towing point located on the porpoise safety panel could cause major canopies during backdown resulting in entrapment instead of release.

Net Depth Effects

As soon as a net is set and pursing begins, the net starts collapsing (i.e., the enclosed surface area decreases). The degree of net collapse that occurs between encircling and releasing the porpoise determines, to a large extent, the probability of prebackdown mortality. The rate of collapse, among other things, is dependent on the depth of the net: The deeper the net, the greater surface area and volume during pursing and throughout backdown. Increased surface area allows the net to remain open longer and reduces the likelihood of porpoise being forced into contact with the webbing due to net collapse.

As part of an experiment conducted in 1979,[8] a 12-strip net was deepened to 14 strips and the increased surface area estimated (Fig. 6). The two-strip addition in depth gave rise to an 11.5% increase in the surface area when pursed and increased fishing depth by 17.2 m (9.4 fathoms). The deepened net could be pursed faster and had a larger backdown channel than the original.

Figure 7 shows a method of deepening the center section of a purse seine by two strips using six equal-length bales of webbing and a 4-mesh, 2-bar taper. This method may be applied to the addition of any even number of bales of equal length to give a two-strip increase in depth. If the bales are each 183 m (100 fathoms) long, the top of the tapered insert will be 220 m (120 fathoms) longer than the bottom side. For example, six 183 m bales, each 100 meshes deep, produce an insert 659 m (360

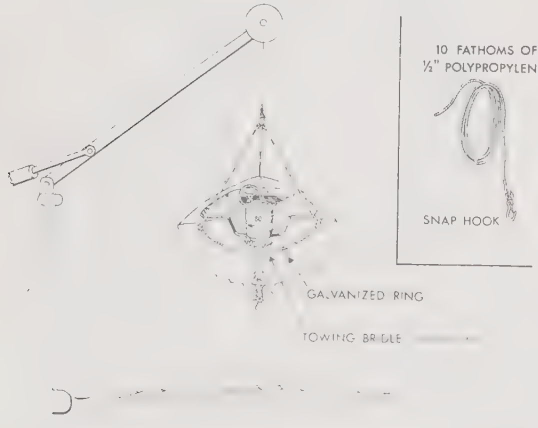

Figure 5.—Rigging for speedboat towing bridle. Note that the galvanized ring is free to slide the entire length of the towing bridle.

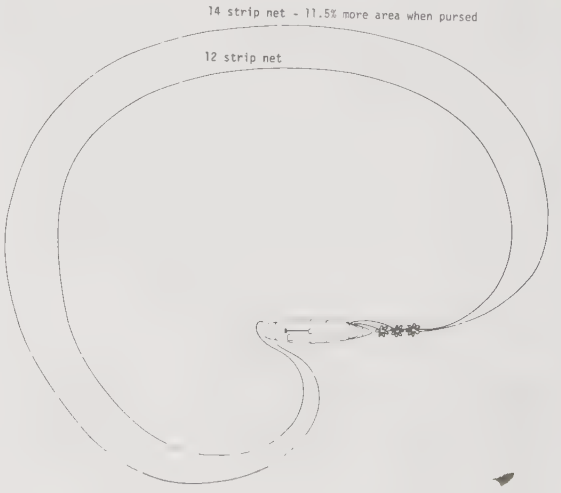

Figure 6.—Deeper nets increase surface area. Actual measurements made during local and at-sea tuna boat charters have demonstrated an 11.5% increase in surface area when pursed by adding two strips to the center of a 12-strip net.

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[8] Unpublished cruise reports: M/V *Cabrillo* May 19, to July 19, 1979 and August 18, to October 7, 1979. On file at the Southwest Fisheries Center, Oceanic Fisheries Resources Division, P.O. Box 271, La Jolla, CA 92038.

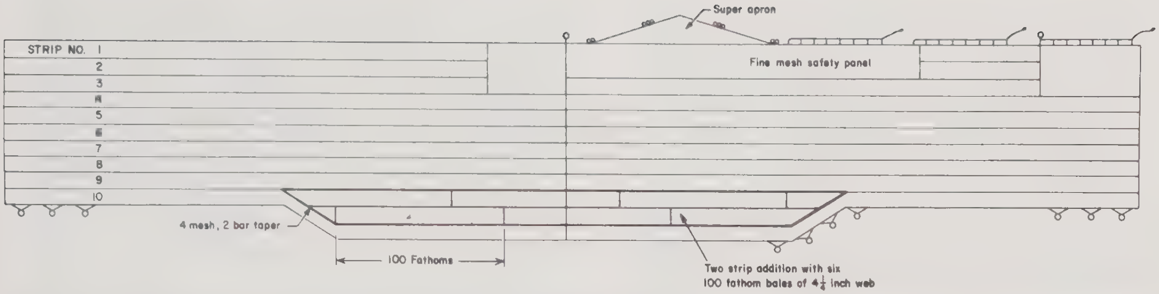

Figure 7.—A two-strip addition in the center of a 10- or 12-strip net can be accomplished with 5, 8, or 10 bales of web, depending on the length of net. The addition is installed between the last strip and the strip above. When only six 100-fathom bales are used, the top edge of the addition will measure 360 fathoms while the shorter bottom edge measures 240 fathoms. Note: New tie-down points must be determined for backdown anytime the depth of the net is changed.

fathoms) long on top, 439 m (240 fathoms) long on the bottom, with two tapered edges of 110 m (60 fathoms) each. If eight 183 m bales are used, the top will be 842 m (460 fathoms) long and the bottom will be 622 m (340 fathoms) long. Nets that are already tapered or are going to be deepened by more than two strips should be examined carefully to decide on the most suitable and economical deepening plan. When deepening a purse seine, it should be kept in mind that nets with a depth-to-length ratio higher than 1:7 may require a slowdown of pursing to avoid excessive strain on the webbing (Fridman 1969).

The Mid-Net Zipper

It has long been suspected that unobserved porpoise mortality occurs in deep areas of the seine prior to backdown. Research divers have observed that the mid-net zipper may hold up a wall of webbing 10 m or more above the floor of the net. This wall, or "mid-net zipper ridge" forms during the pursing operation and persists until that part of the net is retrieved (Fig. 8). Captured porpoise ordinarily concentrate over the deepest area of the net. Consequently, when large numbers of porpoise and tuna are captured they may be forced to cross over the zipper ridge, increasing probability of entanglement or entrapment. Divers have observed porpoise entangled in the overhanging wall of webbing and lesser folds associated with this area (Holts et al. 1979[9]) but, the extent of mortality attributable to the zipper ridge has not been determined.

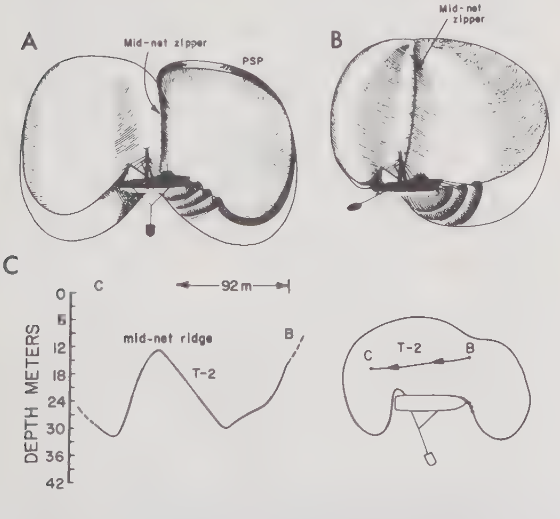

Figure 8.—A. Mid-net zipper ridge when fully pursed. Note indentation of corkline opposite vessel. B. Zipper ridge with one-fourth net retrieved aboard vessel. C. Fathometer trace when fully pursed.

The zipper ridge forms when the "stopper" webbing (a vertical strip of webbing of heavy construction designed to stop rips in the net) is prevented from extending down as far as the adjacent lighter web in the main body of the purse seine. Its formation most commonly results from improper installation of the heavier and stronger "stopper" webbing. Less common causes for the ridge include a short zipper line and incorrectly installed guide rings.

A close look at zipper installation techniques has shown a definite advantage for those seines in which the stopper was installed with an appropriate amount of hang-in slack. While other factors may contribute to restrict full extension of the stopper, one fairly simple adjustment can eliminate them. This adjustment is most easily made at dockside but can be done at sea. The 127 mm (5-in) mesh stopper must be rehung to the 108 mm (4¼-in) mesh with enough slack to permit full extension of the stopper. Here the existing 127 mm mesh stopper webbing is cut out of the seine and rehung, mesh-for-mesh, to the 108 mm mesh. This provides approximately 30% slack in the stopper webbing. An additional one to three meshes of stopper web should be "killed-in" to each strip of the 108 mm mesh. For example, about 4 m of additional slack are provided when only two 127 mm meshes are killed-in for each strip of a 14-strip net. This procedure will ensure a problem-free zipper line by providing for differential shrinkage rates between the 127 and 108 mm mesh, should it occur (Holts 1980).

Downwind Sets

Occasionally, an operator will set the net downwind of the vessel, that is, with the wind blowing the vessel into the net. "Downwind sets" occur very infrequently but can result in a large portion of the captured porpoise being killed. These sets are highly susceptible to net collapse and tend to be more frequent with less experienced captains. Experienced captains will circle around the porpoise school and set when the wind is on the port bow (Fig. 9), insuring that the net circle will be upwind of the vessel, reducing the risk of net collapse.

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[9] Holts, D. B., R. McLain, F. G. Alverson, and J. DeBeer. 1979. Summary of research results from the fifth cruise of the dedicated vessel. November 11 to December 9, 1978. Southwest Fisheries Center Admin. Rep. LF-79-20, 60 p.

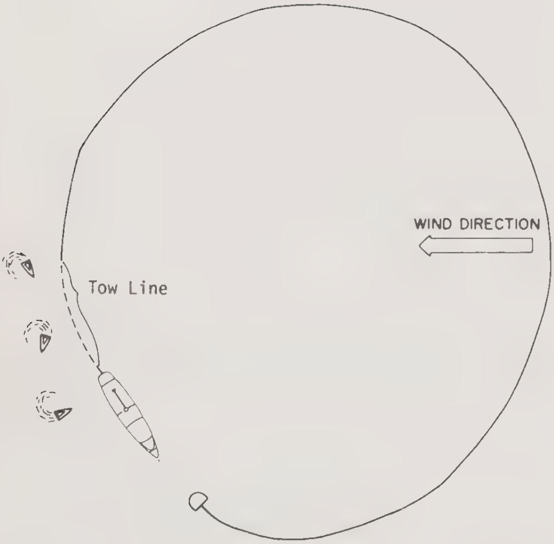
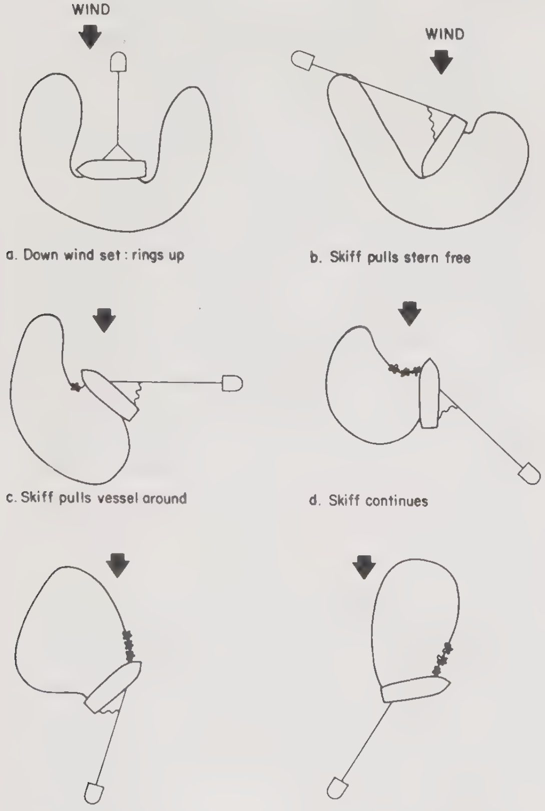


Figure 9.—Always set after turning into the wind. This will keep the net upwind of the vessel.



a. Down wind set : rings up

b. Skiff pulls stern free

c. Skiff pulls vessel around

d. Skiff continues

e. Vessel oriented to wind

f. Vessel ready to backdown

Figure 10.—Procedure for turning vessel around after making a downwind set.

If the net is accidently set downwind of the vessel, the captain must pay particular attention to the developing bow and stern bends in order to maintain near-equal surface areas in each (Fig. 10a). As soon as pursing is completed, the skiff should tow the seiner's stern out and clear of the stern bend in order to avoid possible entanglement on the propeller. As the stern bend is rolled on board (Fig. 10b, c, d), the skiff should begin towing the vessel around until the wind is on the port side. Using the skiff and bow-thruster to move the vessel around to the wind should provide a good net configuration before backdown (Fig. 10f). The biggest danger with these sets is to act too late or not at all.

Using Speedboats to Move Porpoise Inside the Net

Speedboats have long been used to herd and concentrate porpoise in order to encircle them. This is effective because porpoise have a keen acoustical sense and tend to avoid the speedboats. Speedboats are also used during a set to influence the location of porpoise within the net. Circling just outside of the corkline

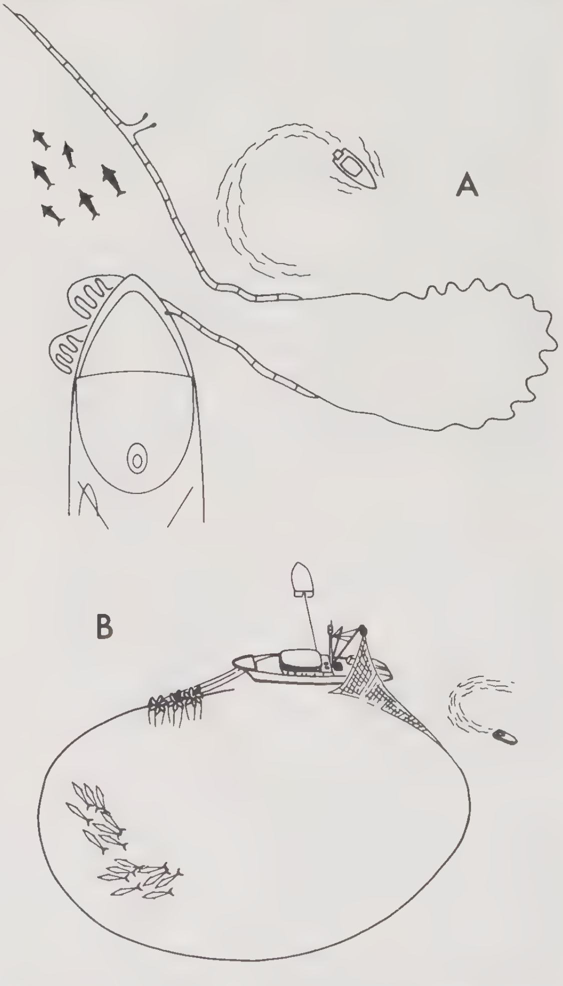


Figure 11.—Use speedboats to prevent porpoise from (A) entering dangerous areas of the net and (B) from entering the area where the corks come out of the water during net roll. Corks make good sonar targets for the porpoise while 108 mm (4¼-in) mesh may not.

discourages porpoise from approaching that area. This tactic is useful for keeping porpoise out of potential danger areas such as bow and stern bends, the bow bunches, and where the net rises out of the water to the power block (Fig. 11). Speedboats should be used whenever possible to discourage porpoise from entering hazardous areas. Speedboats attached to the backdown apex during backdowns, however, should have their motors turned off.

Equipment Malfunctions

The nature of purse-seining operations and the environmental conditions in which they are carried out can lead to gear and equipment breakdowns. These malfunctions do and will continue to occur somewhat routinely on all tuna seiners. They cause porpoise mortality directly through critical breakdowns and indirectly through delays in the net-retrieval procedures. During the period 1977-79, an average minimum of 5.6% of the observed mortality was directly due to equipment breakdowns and gear malfunctions. During this 3-yr period, observed sets with delay-causing malfunctions averaged 19 min longer than sets with no malfunctions.

The role of malfunctions as an indirect cause of mortality may be more important than that of direct causes. The direct influence of hydraulic failures, broken lines, and cables can be readily assessed. But when a malfunction causes an operation slow-down, or change in the net configuration, it is difficult to assess the subsequent contribution to mortality. Therefore, mortality in sets with malfunctions may be attributed to other, more directly observable causes of kill (e.g., net collapse). The percentage of the total observed kill directly caused by malfunctions (5.6%) must therefore be considered a bare minimum.

Table 3 lists the major malfunction categories, frequency of occurrence, percent of malfunction-related kill, and the average delay associated with each. While elimination of all malfunctions is not a reasonable expectation, the frequency and severity of some may be minimized through careful maintenance and inspection schedules.

The proper functioning of a seiner's mechanical equipment is essential both for catching tuna and for safe maintenance and effective release of porpoise. While no specific technology has been developed to reduce the incidence of mechanical failures, machinery critical for porpoise fishing should be inspected more regularly while on the fishing grounds. Maintaining a routine visual inspection and repair policy for all net retrieval systems and speedboats will reduce porpoise kill rates. The most common equipment malfunctions involve speedboats, hydraulic systems, the seine skiff, the various winches, and cable or line failures.

Another class of malfunctions does not necessarily involve the failure of a mechanical system; rather, they result from an ill-defined combination of vessel net characteristics, operator actions, and environmental conditions. These problems include roll-ups (webbing wrapped tightly around the purse cable, preventing pursing) and the entangling of the purse rings in the webbing (preventing net retrieval, after pursing). The propensity for roll-ups seems to be vessel specific and, although a wide variety of informal information on their cause and prevention exists, no technological solution has been devised. In fact, the specific physical causes of roll-ups are not yet fully understood. Tactical methods for avoiding entangling the purse rings in the net may be successful. However, those tactics would be as variable as the environmental circumstances (winds, current profile) which cause the problem. These circumstances and their specific effects have yet to be fully defined.

PORPOISE RELEASE

Backdown is the only proven technique for the wholesale release of captured porpoise. It is also the activity which causes a large share of the porpoise mortality (42% of the kill in sets with kill greater than 15, Table 2). The procedure forces porpoise into contact with the webbing of the floor, side walls, and apex of the channel. Here they may become entangled individually in the meshes, hangings, and holes, or they may become entrapped, en masse, in folds and canopies of loose webbing. Primary factors affecting porpoise mortality during backdown are the configuration of the backdown channel prior to and during backdown, the skill and effort of the captain and crew, the condition of the net, and the behavior of the fish and porpoise. A carelessly executed backdown virtually guarantees high porpoise kill and increases the probability of accidental fish loss.

Condition of Net and Equipment

Failures of hardware components cause loss of valuable fishing time and can lead to the loss of tuna and even other pieces of equipment or the net itself. Similarly, gear failures contribute to kill rates both prior to and especially during backdown. Some commonly occurring gear and equipment problems that contribute

Table 3.—Major malfunction categories showing frequency of occurrence, percent of minimum malfunction-related mortality, and average delay of set for each of the 3 yr of this study.

	1977			1978			1979		
Malfunction	No. sets	Kill %	Avg. delay (min.)	No. sets	Kill %	Avg. delay (min.)	No. sets	Kill %	Avg. delay (min.)
Speedboats	120	9	1	78	2	1	82	13	1
Purse cable	94	13	18	27	15	12	22	24	16
Hydraulic problems	73	5	22	44	5	28	17	5	18
Skiff	63	18	23	35	8	16	29	21	18
Winch and ring stripper	—	—	—	12	2	18	6	3	42
Roll-up	151	12	34	59	12	47	39	17	53
Net tangled in rings	129	13	16	42	29	19	31	5	15
Bow bunches	41	5	6	37	2	16	22	6	15
Other	144	25	20	44	25	12	23	6	16
Total	815	100	19	378	100	19	271	100	19

to backdown-related mortality are set out below with discussions and recommendations where applicable.

Corkline Hangings.—During backdown the weight of the net pulling down on the hangings forms openings between the webbing and the corkline. The 20 fathoms of corkline on either side of the backdown apex are subjected to the greatest downward pull during backdown and at the same time are subjected to maximum porpoise contact. The porpoises' beaks and flippers get caught in these openings, holding the animals securely until they drown or are rescued.

All hangings above the porpoise safety panel and porpoise apron should be tight enough so as not to permit a cylinder of 35 mm (1-3/8 in) diameter to be inserted between the webbing and the floats or corkline. As the fishing season progresses, knots tighten, floats are abraded and compressed, and hangings break, thus producing an increasing number of dangerous openings during backdown. Porpoise caught in these openings increase the job of the rescuers and add to the length of the set. It is strongly recommended that operators ensure that the corkline hangings around the backdown apex are regularly checked by the raft man and maintained in the best possible condition. This task can be simplified by placing the backdown area floats on a lighter auxillary corkline "Medina corkline" and lacing the webbing directly to the main corkline.

Holes in Webbing.—Shark bites, porpoise and fish entanglement, snags during setting and retrieval, as well as many less common abuses contribute to the creation of holes of varying size in the porpoise safety panel and apron. Holes in the backdown area of the net allow fish to escape, porpoise to be drowned, and, because they cause uneven distribution of loads in adjacent areas, tend to get bigger or contribute to the formation of other holes. Aside from the bunt end and the rolling strips, the webbing in the backdown apex bowl (apron and first safety panel strip, Fig. 12) receives the most wear and tear and should get maximum attention for marking and mending of holes. Careful attention should also be given to the lacings between the webbing strips on a vertical line from the backdown apex to the chain since a good deal of the strain of backdown is along this line (Coe and Butler 1980).

The age and degree of use of the webbing in the safety panel and apron greatly affect its resistance to tearing. Three to four years seems to be about the operational life of an apron. It is preferable to replace worn out aprons with new webbing. Segments (bales) in the safety panel can be exchanged from areas of high wear to areas of low wear, to help prolong the service life of the entire panel.

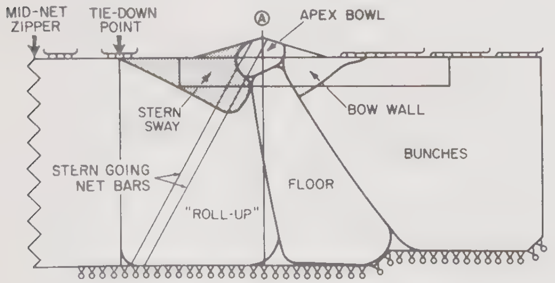


Figure 12.—Functional distribution of webbing in a stabilized backdown channel.

Bow Bunch Failure.—One of the most rapidly wearing components of the backdown system is the outermost bow bunchline. These lines suffer serious abrasion along most of their length by being hauled under load through small diameter steel rings and by being wrapped on a capstan to achieve this hauling power. Typically, bunchlines are 28.6 mm (1-1/8 in) three-strand, twisted nylon rope. After being hauled into its proper position the bunchline is bent sharply over the port rail and secured around a 305 mm (12-in) cleat. The outboard end of the bunchline is usually fastened to a pear link or swivel link and chain by means of a clove-hitch and back-splice. These practices break several basic rules of safe rope use and virtually guarantee a short working life of the outermost bow bunchline.

When the bow bunchline breaks during backdown, backdown must be stopped, the channel collapses immediately, and canopies develop everywhere leading to unavoidable mortality. Under these circumstances the bunchline must be temporarily retied or replaced on the spot, a procedure which is always difficult and often impossible depending on the location of the break. If the bunchline cannot be quickly refitted, the alternative then becomes to release the tie-down, roll an amount of net equivalent to the length of the broken bunch, tie-down again, and back out whatever animals are still left alive in the net.

The probability of breaking the outermost bunchline can be reduced to near zero by handling it slightly differently than is the most common practice. First, use an eye splice with a thimble to connect the bunchline to the swivel or pear link at the outboard end (this may require an increase in the diameter of the outermost bunchline rings). Second, provide a fairlead, roller, or bullnose on the port rail with a diameter three to four times that of the bunchline (10-13 cm; 4-5 in). Third, secure the outermost bunchline on the bow mooring bitt rather than to a cleat. Any sharp bend in a rope under load decreases its strength and may cause premature damage or failure. Most port-side rails and bow cleats in the U.S. fleet create sharp bends and thus contribute to bunchline failure. Even with these precautions, ropes can fail and, so, should be regularly inspected for signs of wear and damage. Further, the terminal chain, its component parts, and bridle splices to the corkline should be examined for weakness or damage on a regular basis. Making the modifications suggested above and frequently inspecting the bunchline and connections will virtually eliminate the infrequent but usually costly consequences of bunchline failure during backdown.

Vessel Control Systems.—These systems are vitally important to the efficient execution of all phases of purse seining, and failure or malfunction in any of them wastes valuable time and contributes to high porpoise kill. Control systems of particular importance for backdown execution are: 1) The net skiff and its towline, 2) the bowthruster and its controls, 3) the vessel gear selector and throttle control, and 4) the rudder control.

Configuration of the Net for Backdown

Dynamics of Backdown.—Any systematic effort to reduce porpoise mortality requires an understanding of the dynamics of the backdown procedure. While each net is different in one respect or another, all nets respond similarly during backdown because they are all constructed of physically similar units (rhombic meshes) oriented in the same direction, with similar external forces working on them. Backing down essentially tows the net by the two ends of the corkline and by the entire bottom of the net (the chain and ring bridles). To achieve the backdown channel configuration that is least likely to kill porpoise, the length of corkline in the water from the outermost bow bunch to the stern tie-down point must be just right. That length is solely determined by the stretched depth of the individual net.

If too little corkline is left in the water, a large apex canopy will form, drowning many porpoise (Fig. 13a). If too much corkline is left in the water for backdown, the apex will fold and wrinkle, and the corks will be difficult to sink (Fig. 13b; McNeely and Holts 1977[10]). When the proper bow and stern tie-down points are used, the backdown apex forms a bowl of fairly taut, open meshes that slopes gently away from the vessel and has no surface canopies. The apex bowl is developed as the water flows against the mesh (apron) at the end of the loop. This bowl is held in place by its connection to 1) the corkline, 2) the vertically stretched webbing between the rings and the apex, and 3) the stern-going net bars from the apex to the chain (to the left in Fig. 12). This 3-point connection is the reason why the stretched depth of the net is so critical in calculating the length of corkline necessary for an optimum backdown channel.

As backdown begins, the net is pulled through the water, causing the meshes to elongate and the net floor to rise. The resistance to the lift being exerted on the net floor results in a downward force sufficient to sink the corkline at the channel apex. This localized sinking is augmented by the weight of porpoise against the webbing below the apex corkline, facilitating porpoise release.

The net floor usually reaches its shallowest point after about 11 min of backing down (Coe and Butler 1980). At this time the subsurface configuration of the backdown channel becomes very stable and the apex corkline becomes more difficult to sink. Every effort must be made to release the captured porpoise as early in backdown as possible. Figure 12 shows the approximate distribution of functional areas of webbing in a stabilized backdown channel (Coe and Butler 1980). Note that the line of force pulling the net through the water causes a large triangle of webbing below the apex and the stern-going net bars to "roll-up" into a long thin sausage shape which spreads out to form the apex bowl. To the bow side of this sausage is the channel floor, which is flat and taut and reaches over to the deeper pocket formed by the slack webbing under the bow bunches. From the stern side of the sausage rises the stern wall which is forced into the channel by the oblique flow of water. The stern wall thus overlaps the sausage and part of the net floor, forming the subsurface canopy known as "stern sway"[11] (Figs. 12, 14). Stern sway disappears where the sausage opens out to form the apex bowl. At present, stern sway is an unavoidable feature of backdown, and may entrap porpoise that stay deep in the channel and fail to move to the apex area as backdown progresses. The faster and more deliberately the early stages of backdown are executed, the less likely it is that animals will become trapped in the stern sway.

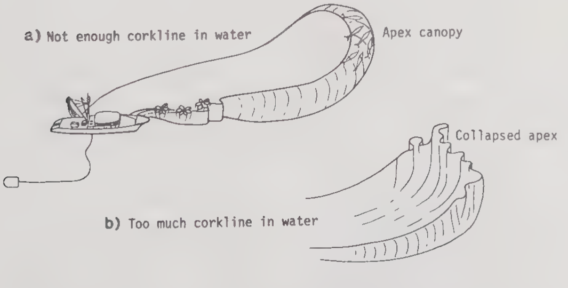

a) Not enough corkline in water
Apex canopy
Collapsed apex
b) Too much corkline in water

Figure 13.—To ensure the proper amount of corkline for backdown, clearly mark tie-down points for the net and last bow bunch pulled. Never estimate these points. The proper amount of corkline is directly related to the depth of the net. Too little corkline (a) in the water will result in apex canopies. Too much corkline (b) will produce a collapsed and wrinkled corkline.

Tie-Down Point Formula.—All vessels installing aprons should perform a water haul (trial set) to locate the proper bow and stern tie-down points for backdown. This insures that the apron apex coincides with the actual backdown channel apex. In order to assist vessel captains and net makers who cannot make trial sets, a series of net measurements for approximating the optimum tie-down points for their nets has been carried out. The results of this work show that the optimum apex to stern tie-down distance is equal to the stretched net depth plus the length of one ring bridle plus the distance from the ring stripper (center) to the point on the port rail where the net is tied during backdown (Fig. 15).[12] It is strongly recommended that the net be tied down as far aft of the ring stripper as possible. The error for this calculation can be up to 3 fathoms, so some minor adjustments to suit individual nets and captains may have to be made after setting the tie-down point.

Table 4 lists the approximate distance from the backdown apex (center of the apron) along the corkline to the correct stern tie-down point for various net depths. When this measurement has been made and the stern tie-down point marked, the outermost bow bunchline can then be adjusted to align the balloons at the apron ends, thereby establishing the bow bunchline mark for a properly aligned backdown channel. From this point, minor adjustments can be made based on net performance and the cap-

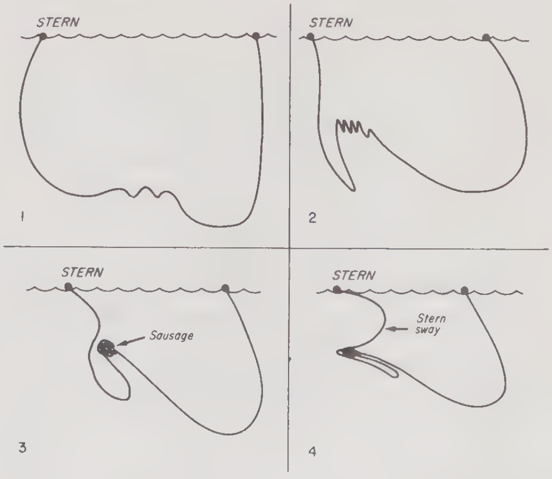


Figure 14.—Backdown channel cross section showing development of stern sway during backdown.

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[10] McNeely, R. L., and D. B. Holts. 1977. Methods of reducing porpoise mortality in the yellowfin tuna purse seine fishery. Southwest Fisheries Center Admin. Rep. LJ-77-13, 19 p.

[11] Unpublished Cruise Report: M/V *Margaret L.*, May 19 to September 11, 1977. On file at the Southwest Fisheries Center, Oceanic Fisheries Resources Division, P.O. Box 27, La Jolla, CA 92038.

[12] Unpublished Cruise Report: M/V *Maria C.J.*, September 12 to December 28, 1980, 25 p. On file at the Southwest Fisheries Center, Oceanic Fisheries Resource Division, P.O. Box 271, La Jolla, CA 92038.

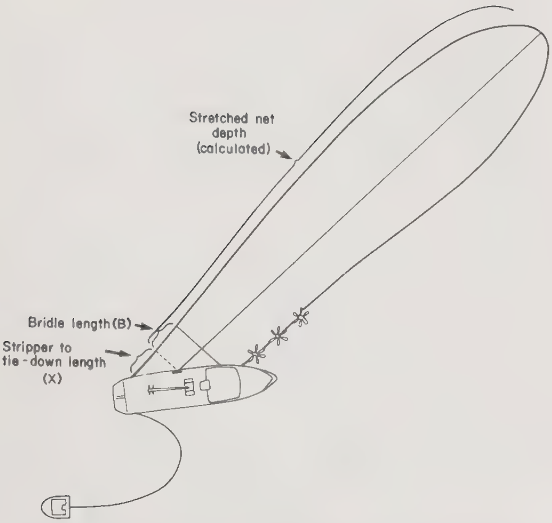
Stretched net depth (calculated)
Bridle length (B)
Stripper to tie-down length (X)

Figure 15.—Determining proper tie-down points for backdown: The sum of the calculated stretched depth (in fathoms), the length of one ring bridle, and the distance from the ring stripper to the point on the vessel where the net is tied down, gives the tie-down point within 4 or 7 m (2 or 3 fathoms).

Table 4.—Calculated distance in fathoms along the corkline from the apron apex to the stern tie-down point. This table is based on nets with 7 to 16 horizontal strips (not counting apron) of 108 mm (4¼ in) stretched mesh web 100 meshes deep plus 2 strips of 32 mm stretched mesh web of 340 meshes with an apron and a salvage 10 meshes deep of 127 to 203 mm (5 to 8 in) stretched mesh and a single purse ring bridle leg of 4 m (2 fathoms).

No. of net strips	Stretched depth (fathoms)	Distance; apex to stern tie-down (fathoms)
9	62.8	62.8 + X[1]
10	68.7	68.7 + X
11	74.6	74.6 + X
12	80.5	80.5 + X
13	86.4	86.4 + X
14	92.3	92.3 + X
15	98.2	98.2 + X
16	104.1	104.1 + X
17	110.0	110.0 + X
18	115.9	115.9 + X

[1] X = distance in fathoms from center of ring stripper to the tie-down location on the port rail (e.g., $X = 0$ if tie-down is under the ring stripper).

tain's preference. This method of establishing tie-down points for backdown is independent of the number of bow bunches pulled. It is based solely on the stretched depth of the net and a known backdown apex location.

The formula for calculating stretched net depth (*SD*) in fathoms as presented in Table 4 takes the form:

$$SD = \frac{(A + B) + \sum_{i=1}^{n} Y_i Z_i}{72}$$

where n = the number of webbing strips of any size or depth between the apron and the chain,

Y_i = the number of meshes deep in the ith strip,

Z_i = the stretched mesh size in the ith strip in inches,

A = the stretched depth of the apron in inches (500-550 or, 0 if no apron),

B = the length of one leg of a ring bridle in inches.

For example, the *SD* of a hypothetical net 15.5 strips deep with no apron and varying mesh sizes would be calculated by the following steps. Starting at the corkline and working down to the leadine (note as a convenience to net makers these calculations are presented in fathoms and inches):

1. Apron depth (*A*) no apron	0 in
2. Two strips, 1¼-in mesh, 340 meshes deep (2 × 340 × 1.254) =	850
3. Three strips, 3-in mesh, 140 mesh deep (3 × 140 × 3) =	1,260
4. Four strips, 4¼-in mesh, 100 meshes deep (4 × 100 × 4.25) =	1,700
5. Six and one-half strips, 5-in mesh, 100 meshes deep (6.5 × 100 × 5) =	3,250
6. One salvage strip, 8-in mesh, 20 meshes deep (1 × 20 × 8) =	160
7. Single ring bridle length (*B*), 3 fathoms (3 × 72 in/fathom) =	216
8. Adding items 1 to 7 =	7,436 in
9. Dividing 7,436 in by 72 in/fathom yields:	*SD* = 103.28 fathoms

By following this method, the stern tie-down point to backdown apex distance on the corkline can be approximated for any net and vessel combination by adding the distance, in fathoms, from the center of the ring stripper to the tie-down location on the port rail (*X* in Table 4 and Fig. 15). It is absolutely essential that the net structure (strips, meshes deep, and mesh size) between the backdown apex and the chain be known precisely.

Porpoise Safety Panel.—Since 1977, Federal regulations have required a 32 mm (1¼-in) stretched-mesh safety panel in the backdown area. The employment of small mesh protection against entanglement (Barham et al. 1977) has been a major factor contributing to the drastic reduction of average kill rates from 1976 to the present.

The required safety panel for most seiners is a minimum of 330 m (180-fathom) stretched length (before installation) by two full strips of 32 mm mesh. Typically, the safety panel consists of six bales of webbing, each 110 m (60 fathoms) long by 340 meshes deep, laced together in a rectangle 3 bales long and 2 bales deep (Fig. 16). Because 340 meshes of 32 mm stretched mesh webbing is equal in depth to 100 meshes of 108 mm stretched mesh (a standard production size), the safety panel is conveniently installed by replacing the top two strips of 108 mm mesh directly below the corkline around the backdown channel (Fig. 17). The specific location of the safety panel in the net is partially determined by Federal regulations in that it must cover at least two-thirds of the stern side of the backdown channel and extend around the channel to a point 110-183 m (60-100 fathoms) from the bow end of the net (ortza). The bow end of the safety panel should completely cover the outermost bow bunch that is pulled for backdown. Further, all operators must understand that the length of corkline around the backdown channel is dependent on and determined by the stretch depth of the net (see Tie-Down Point Formula). This is true even if the net does not have an apron.

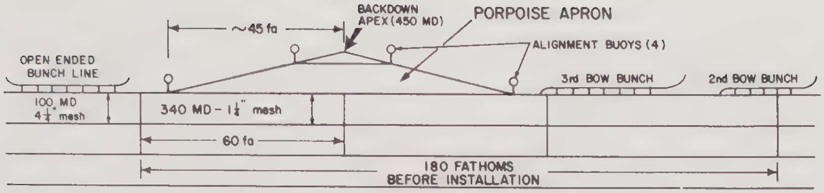
BACKDOWN APEX (450 MD)
PORPOISE APRON
~45 fa
ALIGNMENT BUOYS (4)
OPEN ENDED BUNCH LINE
3rd BOW BUNCH
2nd BOW BUNCH
100 MD 4½" mesh
340 MD - 1¼" mesh
60 fa
180 FATHOMS BEFORE INSTALLATION

Figure 16.—Configuration of porpoise safety panel and super apron.

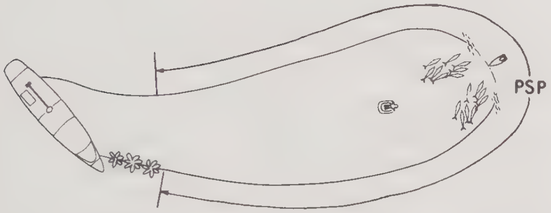

Figure 17.—Porpoise safety panel (PSP) must cover the perimeter of the backdown channel, at least from the last bow bunch pulled, around the apex and sternward at least two-thirds of the distance back along the sternside of the channel.

For those seiners without aprons, having more than one set of tie-down points can be useful. In order to backdown successfully with varying numbers of bow bunches pulled, pairs of clearly marked tie-down points must be established for each apex location desired. The safety panel should be lengthened to ensure complete coverage of the backdown channel's perimeter in each backdown configuration. The pairs of marks (stern-side corkline and outermost bow bunchline) must be clearly distinguishable (numbered or color coded) to avoid serious errors in tie-down combination (Fig. 18).

Super Apron.—The super apron, or simply the apron, as it has come to be known, is a triangular-shaped section of 32 mm (1¼-in) webbing approximately 165 m (90 fathoms) long at the base and 450 meshes high at its peak (Fig. 16). It is installed between the corkline and the upper edge of the porpoise safety panel in a location that places the peak of the triangle at the desired backdown channel apex. The apron has several advantages in that during backdown it forms an inclined ramp which helps deliver the porpoise to the release area at the backdown apex, it reduces the tendency for slack webbing to develop into canopies along the sides of the backdown channel near the apex, and it adds another strip-and-a-third of small mesh to protect the floor and sides of the channel from porpoise entanglement. Another positive feature of the apron is that its required use has forced vessel operators to locate and use their optimum tie-down points. This has certainly resulted in far fewer porpoise deaths due to unnecessary canopies in poorly configured backdown channels.

The construction of an apron requires one 110 m (60-fathom) by 340-mesh bale of 32 mm webbing. Instructions for building and installing an apron are provided by Holts (1977[13]).

Executing Backdown

The use of right rudder, thrusting to port, and briefly towing the stern to starboard with the skiff at the start of backdown can help to quickly set up the channel in the correct position for porpoise release. The skiff and bowthruster should be used as needed prior to tie-down to gently begin stretching the net and positioning the vessel for the start of backdown. This pre-forming of the channel will help ensure that porpoise are at or near the apex when backdown begins, thus contributing to rapid, en masse release.

Care must be taken to ensure that the net will not fold in on itself when backdown begins because this malformation of the channel can result in high kills.[14] Therefore, the captain should use a speedboat to pull the corkline out whenever it is folded into the channel (Fig. 19). Bunchlines must be arranged so that the bow bunches are evenly spaced and fall in the natural line of the bow corkline from the apex to the breastline attachment. Improperly aligned bunches will either reduce the volume of the bow

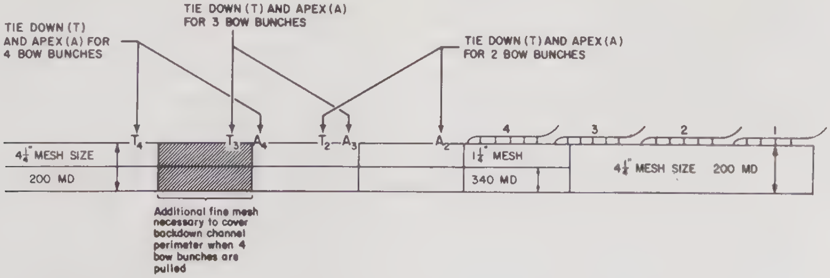
TIE DOWN (T) AND APEX (A) FOR 4 BOW BUNCHES
TIE DOWN (T) AND APEX (A) FOR 3 BOW BUNCHES
TIE DOWN (T) AND APEX (A) FOR 2 BOW BUNCHES
T4
T3
A4
T2
A3
A2
4
3
2
1
4¼" MESH SIZE
200 MD
1¼" MESH
340 MD
4¼" MESH SIZE 200 MD
Additional fine mesh necessary to cover backdown channel perimeter when 4 bow bunches are pulled

Figure 18.—Multiple tie-down points for backdown in nets without aprons when using 2, 3, or 4 bow bunches. Remember to avoid placing bunchlines within 18 m (10 fathoms) of any of the apex markers.

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[13] Holts, D. B. 1977. The super apron system: Construction and installation. Southwest Fisheries Center, Admin. Rep. LJ-77-30, 12 p.

[14] Unpublished Cruise Report: M/V *Bold Contender*, September 22 to December 4, 1975, 13 p. On file at the Southwest Fisheries Center, Oceanic Fisheries Resource Division, P.O. Box 271, La Jolla, CA 92038.

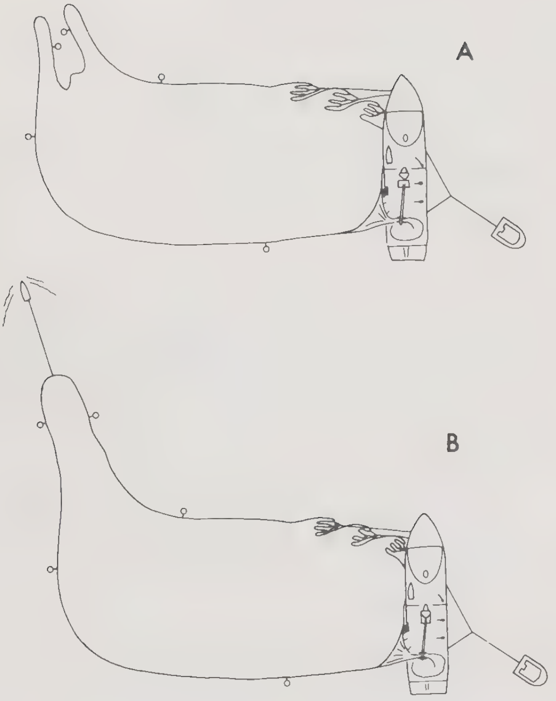

Figure 19.—Straighten out the channel apex before backdown. Do not attempt backdown when the apex is folded into the net. Use a speedboat to pull out collapsed section before attempting backdown.

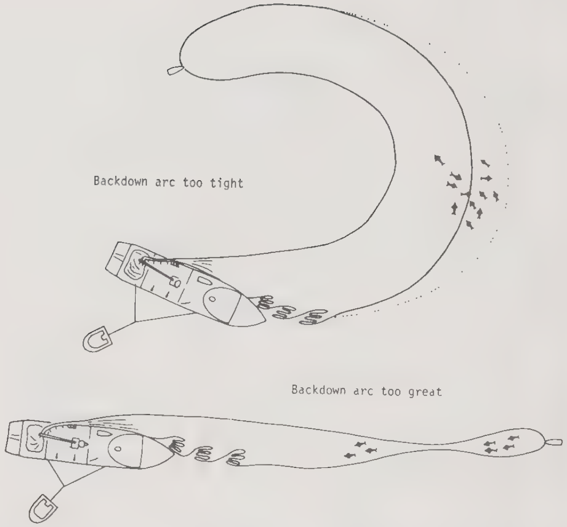

Figure 20.—Proper backdown arc insures efficient waterflow to maintain a wide and deep channel. Maintain correct radius of turn by changing the pulling position of the net skiff, rudder angle, and direction of bow thruster as necessary.

side pocket for the fish or create canopies along the bow wall of the channel, both of which increase the difficulty of backdown and increase the probability of porpoise kill. The outermost bow bunch should be positioned no farther out in the channel than one-third of the distance from the bow to the apex and should be fully protected by the porpoise safety panel.

Maintenance of an open and canopy-free backdown channel requires careful control of the arc that the vessel makes while towing the net (McNeely and Holts footnote 10). This natural arcing tendency can be reduced or augmented depending on its suitability for channel operation. If the arc is too tight (i.e., the channel is too curved), bow side canopies will be present and the corkline won't sink at the apex (Fig. 20a). If the arc is too straight, the channel will quickly collapse and porpoise will create canopies by being overcrowded (Fig. 20b).

Not infrequently the lack of adequate communication between the captain and the speedboat operator at the backdown apex has resulted in either accidental fish loss or the failure to release all of the captured porpoise. This problem is particularly apparent during night backdowns when hand or flashlight signals are difficult to see and interpret. To relieve this problem, two-way radio communication may be set up between the apex-tending speedboat operator and the captain. During night backdowns a powerful floodlight should be continually shown in the area of the bow bunches in order to attract and possibly hold some of the fish in the net pocket below the bunches. A hand-held spotlight should be used only as needed by the speedboat driver at the apex to determine how many porpoise remain in the net. Intermittent spotlighting of the apex area from the main vessel should be kept to a minimum as it temporarily blinds the speedboat operator and any rescuers in the area. Floodlighting of the entire net using a diffuse light source may eliminate some of the problems caused by poor visibility during night backdowns.

Another speedboat can be used during backdown to circle in the area of the bow bunches and discourage porpoise from swimming upstream, away from the apex release area. The backdown operation should be continued until all the porpoise are released. Since the apex corks become progressively harder to sink after the channel stabilizes (about 11 min), aggressive, nonstop backdown should be continued as long as there are enough porpoise in the net to plug the apex and prevent fish release. As the channel narrows, the release area gets smaller, and requires fewer porpoise to fill in the release area and prevent fish loss (Coe 1976[15]). Thus rapid backdown can continue until very few porpoise are left in the net. These are general recommendations and must be tailored to particular circumstances in the field.

Rescue by hand should be continued to ensure that zero-kill sets occur as frequently as possible. Diving and depth recording instruments show that within 1 min after the vessel stops backdown, the channel floor sinks from 4-6 to 20-25 m. This rapid increase in net volume gives any live porpoise remaining in the net a tremendous amount of space in which to avoid rescue attempts. For this reason, backdown should be continued, at least slowly, until rescuers have removed all live porpoise from the net.

When all the captured porpoise have been released it is common practice to release or partially release the outermost bow bunchline. This action takes the tension off the apex area of the channel and helps to ensure that the corkline will not accidentally sink and release fish. The vessel should continue to backdown slowly until the wind is on the port bow. At this point backdown can stop and net retrieval can be resumed.

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[15] Coe, J. M. 1976. The effectiveness of the porpoise apron in improving the backdown prodecure. Southwest Fisheries Center, Admin. Rep. LJ-76-38, 17 p.

Porpoise Behavior During Backdown

There are several aspects of porpoise behavior that are relevant to their release or rescue during backdown. This information is presented so that participants in the fishery may have a better understanding of some of the causes of mortality that are uncontrollable as well as the behaviors that supplement the release and rescue efforts.

Most porpoise (especially spotters) display a behavior termed "rafting" (Norris et al. 1979[16]). Rafting occurs when individuals or groups of porpoise remain at the surface or just below it for long periods of time with a minimum of swimming and virtually no diving activity. Typically, the rafting animals are motionless at the surface with the head up and tail down. Rafting groups can involve any proportion of the school and are nearly always composed of pure spotters. Rafting usually begins after the rings are up and increases until backdown disrupts it.

Since rafting animals move very little, they can be positioned at or near the apex for the start of backdown by using the skiff to slowly stretch the bow corkline during net rolling and pull the net to the porpoise. When backdown begins the rafting groups drift up to the corkline where they may become more active in an attempt to avoid the advancing wall of net. By this time it is too late for the rafting animals to avoid the net because those nearest the vessel keep drifting against the animals nearest the apex, forcing their release over the corkline. It seems that as long as there are rafting animals on the boat side of the porpoise at the apex corkline and there are no major disturbances to cause these rafts to break up, this "passive crowding" effect will operate and the porpoise will be easily released. Unnecessary noise or other stimulation during the set should be avoided in order to enhance the generally inactive state of the porpoise and get the maximum benefit from passive crowding during backdown.

Backdown release becomes more difficult when the remaining porpoise are aware of the advancing apex corkline. At this point the animals will swim upstream, away from the apex where they may fight the net at the surface (or at depth), passively allow themselves to be dragged along with the net, or actively attempt to get over the corkline.

Porpoise in the captured school either swim actively from the advancing wall of the net, raft, or display what is termed "passive" behavior (Coe and Stuntz 1980). During backdown there are occasionally some animals that sink and lie on the webbing and many more that show signs of the sinking behavior and drop out of the rafting groups. At first glance, the animals appear to be struggling feebly, perhaps against the current being produced as the seine is pulled through the water during backdown. Their movements are weak and lack the grace that one expects in porpoise. After about 3-5 min, the passive porpoise begin to rise singly or in two's and three's to breathe and are either backed out of the net or hand-released if the backdown procedure has already been terminated. Animals usually do not return to rest on the bottom of the net after surfacing.

When viewed from a speedboat tending the corkline in the release area during backdown, animals may appear to be dead, and as a result the release efforts may be prematurely terminated. Porpoise not released during backdown have a high probability of being killed. The reasons for passive behavior in purse seine-caught spotters are not fully understood and this behavior has only rarely been observed in spinners.

Porpoise cannot swim backwards. Once in a canopy they rarely get out unless they either sink free due to exhaustion or passive behavior, are rescued, or have the canopy pulled past them such as in a bow or stern wall canopy during backdown.

A very large catch of fish may cause fragmentation of the porpoise school and result in groups being caught in the meshes deep in the net prior to backdown. Large catches may also cause some of the porpoise to enter deep canopies near the boat during backdown or to get caught under the bow bunches. Little can be done to avoid these occurrences, but increased rescue effort, such as using a second raft, may help to minimize the resultant mortality. The number of porpoise killed in a set is highly correlated with the amount tuna caught. That is, with increasing tuna catch one can expect release to be more difficult, increased rescue effort to be necessary, and a higher likelihood of unavoidable kills.

Trouble Shooting Backdown Performance

Skipper interviews, observer data, and field observations point out several common and recurring problems with backdown performance. These are identified and discussed in this section.

1. Inability to sink the corkline at the backdown apex is one of the most common and frustrating problems that occurs. It causes higher than normal kill rates, protracted backdown times, and high levels of hand-rescue effort. There are two causes for this complaint. The most frequent is the stabilization of the channel configuration after 10 or 11 min of backdown. Stabilization of the channel is unavoidable due to the physical structure of the net and its reaction to induced water flow. However, there are several techniques to help reduce its consequences.

First, backdown faster and more aggressively before the channel stabilizes, so that most, or all, of the porpoise are out of the net while the corks will still sink.

Second, slightly more downward force on the corkline can be generated after stabilization by having a little less corkline in the water. Shorten the corkline in the backdown channel by increments of 1 fathom at both the stern and bow bunchline tiedown points. Continue shortening the corkline in this manner, 1 fathom during each set until the desired results are achieved. If a slight canopy forms at the apex, slack off a few fathoms from both the bow and stern and discontinue this method.

Third, assuming the remedies outlined above failed to produce the desired results, begin removing flotation from the apex area. Do this carefully and only as a last resort, because removing floats to enhance late backdown sinking will enhance the ease of sinking and the difficulty of raising the corkline in early backdown.

2. Surface canopies are a common cause of porpoise mortality during backdown. In a properly configured backdown channel, they are ordinarily formed when the porpoise swim against the webbing along the walls of the net. In the case of canopies on either side of the channel, the captain's most immediate job is to continue backing down as fast as possible to cause the animals to slide down the channel toward the apex. If there is a canopy at the apex of the channel, then the net is improperly tied down and more corkline must be put into the loop. This should be done in steps of 2-4 m (1-2 fathoms) from both bow and stern until the apex canopy no longer forms. In any particular instance an apex canopy can usually be relieved by slacking the outermost bunchline a few fathoms and continuing the backdown. However, adjustment of this bunchline during backdown is not a solution to

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[16] Norris, K. S., W. E. Stuntz, and W. Rogers. 1978. The behavior of porpoises and tuna in the eastern tropical Pacific yellowfin tuna fishery-preliminary studies. Available U.S. Dep. Commer, Natl. Tech. Inf. Serv., Springfield Va., as PB 283970, 86 p.

consistent apex canopy problems. Adjustment of the stern corkline mark and the outermost bow bunchline mark to put more corkline in the water should permanently solve the problem.

Major bow-side canopies are usually the result of too tight an arc for backdown, which causes an oblique water flow and pulls the bow corkline over the surface of the channel. The use of more right rudder to decrease the backdown arc is useful in straightening out the channel while continuing to backdown.

Consistent bow-side canopies may be due to differences in hang-in rates caused by the improper installation or reinstallation of a porpoise apron that required the "killing-in" of large amounts of webbing. Check the hang-in in any areas with consistent localized canopies and correct it so that the entire bow wall has the same hang-in rate.

Stern wall canopies during backdown are almost entirely caused by the porpoise themselves due to crowding or in avoidance of fish. At present there is no remedy other than to continue rapid backdown to flush the porpoise to the apex and to check the hang-in rates in areas with consistent localized canopies.

Once begun, backing down should never be completely stopped because the tension goes off the meshes and animals can then push against the webbing and form a canopy anywhere in the net. By the time backdown is resumed, it may be too late to back the animals out of their self-formed canopies. This same problem occurs with tuna and can result in pockets of dead fish that slow net retrieval after backdown. Furthermore, if porpoise hit the net in areas of 108 mm (4¼-in) mesh while it is slack, their beaks will go through and when tension is reapplied, the mesh will stretch and close, holding the animal in place.

3. Backdown-channel collapse is a fairly common occurrence at the end of the maneuver and is usually only partial. If all or nearly all of the porpoise are out of the net at the time of partial collapse, it is of little consequence and, in fact, helps rescuers get their hands on the stragglers for quick rescue. Once the wind is on the port bow and net rolling begins, the channel should open immediately, providing room for the live fish to circulate.

If channel collapse occurs early and consistently in backdown, the cause is usually too little arc in the path of backdown (i.e., it is too straight) and is remedied by moving the rudder more to port and, if necessary, thrusting the bow to starboard (McNeely and Holts footnote 10). Channel collapse, especially at the apex, can occur if too much corkline for the amount of webbing is in the water. This can be remedied by shortening the corkline by increments of 2 fathoms. This must be done carefully since pulling too much corkline, or pulling it unevenly, will create canopies at the apex.

If increasing the backdown arc and shortening the corkline loop do not solve the early backdown-channel collapse problem, the stern tie-down location may be removed as far aft on the port rail as possible. If this is done, the stern tie-down mark will also have to be moved an equal distance.

4. Sinking of the corkline on the bow side of the channel in the early stages of backdown is usually a harmless though aggravating characteristic of the backdown procedure. In some instances, where porpoise start to leave the net in this area, problems can develop when the net straightens out and these corks no longer sink. Some porpoise, expecting to follow those just released, can become entrapped under that area of the net. This problem can be reduced by trying to stretch out the bow corkline and getting the boat in line with it before applying power for backdown. The skiff can help orient the boat and stretch the bow corkline during net rolling just before backdown so that no time is wasted.

5. When these remedies have been tried without success or the solution to one problem gives rise to another, it is time to consider the balance of chain and corkline at the stern tie-down point. If the chain is 18-36 m (10-20 fathoms) ahead or behind the corkline at the tie-down point, the backdown channel may be seriously affected. Problems stemming from the corkline or chain consistently falling behind can usually be remedied by adjusting the angle of the power block. For example, when the corkline is falling behind the chain, adjust the power block to allow the chain to drop into the bottom of the "V" (inside) while the corkline is on the outside riding over the top of the webbing. This allows the corkline to come aboard at a faster rate than the chain. If the chain/corkline cannot be balanced in this way then a sling can be used to bunch 5-8 m (3-4 fathoms) of corkline at a time until the proper balance is achieved. The original stern tie-down mark on the corkline must be used to preserve the proper location of the backdown apex. Adjusting the corkline/chain balance only influences the amount of webbing and its configuration in the water.

Porpoise Release Without Backdown

On the rare occasion where backdown cannot be performed, the only reasonable way to release the captured porpoise also releases the fish from the net. However unsatisfactory this alternative may be, it is recommended that it be carried out to avoid drowning most of the mammals. After the contents of the net are released, the cause for the inability to backdown can be repaired and, if enough daylight remains, the school may be recaptured.

To accomplish this release, roll the net until the area is approximately equal to or smaller than that for a normal backdown (depending on the number of porpoise captured), while trying to keep the net shape as rounded as possible. The bow ortza and breastline are passed to the net skiff and the bottom six to eight purse rings on the ring stripper are cut loose from their bridles. If possible, the breastline should be reattached at the ortza before transferring it to the skiff. If the bow bunches have already been pulled in, the bunch lines should also be passed to the skiff at this time. The skiff should then idle away from the bow to a distance of about 55 m (30 fathoms) and try to hold that position. If the skiff gets too far from the ring stripper, the chain (leadline) between the stripper and the skiff will rise, reducing the size of the opening for porpoise release. One or two speedboats should circle slowly outside the corkline on the stern side of the net to help move the porpoise toward the opening. It may take some time for the animals to start to leave the net. A raft and rescuer should be in the water on the stern side of the porpoise in case of entanglements or formation of canopies.

While the net is in this configuration, it is recommended that it be rolled to squeeze the porpoise out only as the very last resort, in which case more rings should be dropped. Since there is no skiff to control the position of the boat, rolling the net will cause the opening to become more shallow by pivoting the boat and may also force the porpoise into canopies as the stern moves toward them. Throughout this operation, the strength and direction of the wind will determine specifically how the skiff, vessel, and net will be maneuvered to maintain the release opening.

In the case where only a few porpoise have been captured, a raft man or two can attempt to rescue them by hand prior to opening the net. If they are successful in this attempt, any fish captured can be retained.

PORPOISE RESCUE

Each tuna seiner engaged in fishing for tuna in association with porpoise should have at least one inflatable raft for use as a porpoise rescue platform during and after the backdown procedure (Coe and Vergne 1977). The following guidelines are recommended for raft use.

Equipment for Raft Rescue

1. The raft should be at least 2 m long, with a double bladder inflating system which can be rigidly inflated and durable enough to withstand sun as well as deck and net abrasion. A back-up raft and repair kit should be on board.
2. A mask and snorkel are required to give the rescuer a clear view of underwater porpoise activity. Spotted porpoise occasionally "play dead" (passive behavior) by lying against the webbing during backdown and may be thought dead unless viewed underwater with a mask and snorkel. The raft man and his alternate should personally acquire their masks and snorkels to ensure proper fit. Low volume, three-window masks with a purge valve seem best suited for this activity.
3. A snap hook attached to the bowline of the raft about 2-4 m (1-2 fathoms) from the bow will allow rapid attachment and detachment from the corkline during rescue maneuvers. This hook should be used at all times during backdown.
4. Cotton gloves should be worn to give the necessary grip on the slippery beaks of the porpoise.
5. A wooden canoe paddle or its equivalent will allow the rescuer to paddle to the corkline.
6. The rescuer should be an experienced swimmer, who is individually motivated to get the live porpoise out of the net. One rescuer per raft is more efficient than two, because stability and mobility are maximized.

Techniques of Raft Rescue

During backdown, the snap hook on the raft bowline should be attached to the corkline or webbing about 9-18 m (5-10 fathoms) from the apex on the stern side. From this vantage point the rescuer may observe the entire backdown and signal when the channel is clear of fish and when all live porpoise have been released. If the raft man is sufficiently skilled, he may paddle to the center of the channel and hold position, thereby helping to keep the porpoise from swimming upstream. In doing this, he should try to stay at least 10 m upstream from the closest porpoise.

As backdown nears completion, the rescuer should detach the raft, move to the apex of the net, and reattach so that he can disentangle and remove any remaining live animals. The rescuing process is made easier if the vessel continues slowly astern; this helps keep the porpoise at the end of the net and within reach. Every effort should be made to remove all of the live porpoise before ceasing backdown. Should any animals remain in the net after backdown, the rescuer can sometimes move down the corkline and drive the porpoise onto shallow webbing or back to the apex where they can be caught and released. Rescue efforts should be carried on until all porpoise are removed or the net skiff comes around. Although it is commonly done, using the raft after dark or leaving the raft to rescue porpoise by swimming is not recommended. At any time during a set, the raft may be launched to rescue porpoise or to clear fouled bunchlines. In sets where backdown is hampered or impossible, a rescuer, wearing a mask and snorkel, operating from a raft can be instrumental in reducing an otherwise certain high kill. Hand rescue efforts can make the difference between an above average kill and zero kill in many sets.

ROLE OF THE CAPTAIN AND CREW

The successful execution of backdown and, for that matter, the entire purse seining operation, depends on the level of skill, motivation, and effort of the captain and crew. The captain has overall responsibility for initiating and directing the seining operations but cannot personally supervise each specific action by each member of his crew. Therefore, however broad or narrow responsibilities may be, each functioning member of the crew must 1) recognize circumstances requiring action, 2) know what action is required or to whom to report the circumstances, and 3) be able to execute the necessary action effectively. It is the captain's responsibility to ensure that his crew is competent and replace or train those who are not. The proper blend of skill and responsibility will inevitably lead to a highly competitive, self-motivated, and successful team.

The high rate of exchange of captains and crew among vessels detracts from the overall proficiency of execution of operations, and reduces the level of equipment maintenance. The operation and handling characteristics of each vessel and net combination necessitate a learning period. During this period, hitches in the operation, gear malfunctions, misinterpreted orders, etc. cause increased porpoise kill. Whenever a captain changes vessels, with or without changing crew, at least one trial set, with backdown, should be performed. By performing a trial set(s), the new captain may be able to identify specific vessel control characteristics for backdown, generally review crew performance, alter any aspects of the operation for greater efficiency, and have the chief engineer and deck boss identify any gear or machinery in need of attention.

Utilization of the information presented here will help lead to the lowest possible porpoise mortality rates achievable with the present state of purse seining technology. The maximum possible exchange of information, techniques, and ideas among the captains in the fleet is essential for the maintenance of low kill rates. The Expert Skipper's Panel (ESP), established through the American Tunaboat Association, is an excellent source of information for captains desiring to improve the efficiency of their fishing operations, especially on schools of porpoise. The ESP can help analyze the causes of problems in gear or procedures and make practical suggestions for their remedy.

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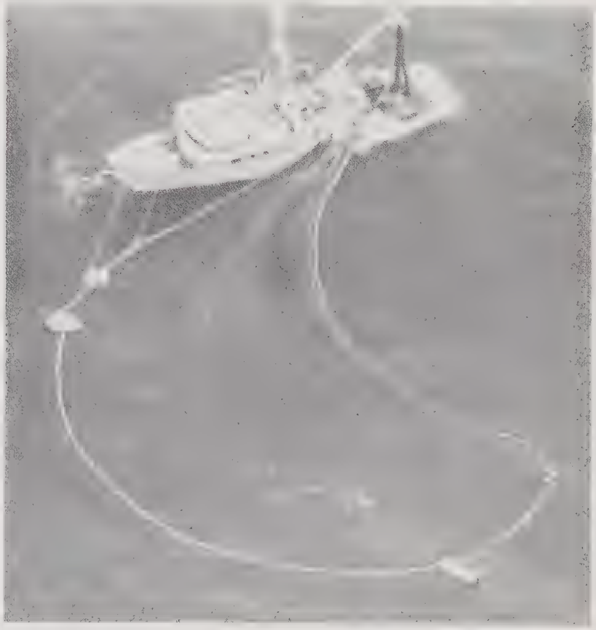
The "Tuna-Porpoise" Problem: NMFS Dolphin Mortality Reduction Research, 1970-81

JAMES M. COE, DAVID B. HOLTS, and RICHARD W. BUTLER

Introduction

Nearly 15 years have passed since the National Marine Fisheries Service (NMFS) first became concerned with reducing incidental dolphin[1] mortality in the U.S. tuna purse-seine fishery. This paper is presented as an overview of NMFS' applied research on this problem. The major portion of this research was conducted at the La Jolla Laboratory of the NMFS Southwest Fisheries Center (SWFC). This paper is not intended to be a complete history of the program, but rather is a summary and index of the major research conducted by the SWFC over the full course of the program's existence from 1970 to 1981. A glossary (Table 1) and a bibliography of NMFS publications and reports on dolphin mortality-reduction research are included.



A typical purse seine during the backdown procedure.

The Vessel is a 525-ton class III seiner which is beginning backdown with about 200 spotted dolphins in the net.

Background

Purse seining for yellowfin tuna, *Thunnus albacares,* in the eastern tropical Pacific reached commercial proportions in the 1950's (McNeely, 1961). This fishing method involved the incidental deaths of many thousands of dolphins, a fact not widely known until the late 1960's (Perrin, 1969; 1970). In 1969 a modest research program was formed within the National Marine Fisheries Service (then named the Bureau of Commercial Fisheries) to investigate the specific nature of what has since come to be known as the "tuna-porpoise" problem. From its inception, this research program, located at the NMFS Southwest Fisheries Center, has had a portion of its resources dedicated to research on the reduction of incidental dolphin mortality in the tuna fishery.

The Marine Mammal Protection Act (MMPA) of 1972 charged the NMFS with the responsibility of carrying out provisional regulations designed to reduce dolphin mortality and injury to the lowest practicable level. In 1972, while this act was being drafted, NMFS convened a group of marine mammal scientists, fishery biologists, and policy specialists, known as the NOAA Tuna-Porpoise Review Committee, to prepare an action plan addressing the tuna-porpoise problem. The report of this group[2] provided general guidelines under which virtually all subsequent NMFS dolphin related research has

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[1] Three species of pelagic dolphins (commonly called "porpoise" by tuna fishermen) were primarily involved in this research. They are, in order of decreasing importance, the spotted dolphin, *Stenella attenuata;* spinner dolphin, *S. longirostris;* and the common dolphin, *Delphinus delphis.* Common names in this paper for marine mammals follow the terminology of the International Whaling Commission and the U.S. Marine Mammal Commission.

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[2] Report of the NOAA Tuna-Porpoise Review Committee, Sept. 8, 1972. U.S. Dep. Commer., NOAA, NMFS, Southwest Fish. Cent., La Jolla, Calif., 63 p.

Table 1.—Glossary of tuna seining terms and definitions adapted from F. M. Ralston (editor), 1977. A workshop to assess research related to the porpoise/tuna problem. SWFC Admin. Rep. LJ-77-15, 119 p.

Apex flapper: An experimental modification to the super apron consisting of a series of overlapping, trapezoidal pieces of 1¼-inch mesh. These panels were placed above the corkline at the apex of the backdown channel to provide a visual barrier to the tuna and, at the same time, be permeable to dolphins.

Apron: A trapezoidal appendage sewn to the top edge of the uppermost dolphin safety panel(s) of a purse seine. Before the apron can be installed the corkline must be cut from the safety panel. The corkline is subsequently reattached to the sides (which are equilateral) and the top of the apron, the base of the apron having been attached to the safety panel. The apron produces a ramplike shallowing of the backdown area, reduces canopies, and reduces the incidence of tuna mixing with the dolphins in the release area during backdown.

Backing down (backdown): A process whereby the corkline of the purse seine can be submerged and pulled from under the dolphins with the application of reverse engine power by the seiner. This is a fundamental technique for releasing dolphins from the net.

Bridles: Typically, these are sections of chain that are attached at both ends to the seine chainline. They are cut at a length that allows draping of the bridle below the chainline; a split-link is attached at the center of the bridle and a pursing ring is tied to this link (also see towing bridles).

Bunches: These are large clumps of bunched corkline. They are pulled using an auxiliary bunch-line (like a draw string) that runs through small (3″ diameter) rings which are tied to the corkline. Bunches are useful in 1) removing excess slack in the corkline (which can lead to canopies and entrapment) and 2) maximizing the bouyancy of the net going into the sacking-up phase (to prevent sinkage and loss of fish).

Canopy: This is a configuration where the webbing blossoms out beyond the corkline due to currents or other adverse conditions. Dolphins in canopies frequently can't find the way back to the surface to breathe due to the sometimes convoluted shape of the canopy. Canopies can also be caused by net collapses, where the corkline comes together and forces dolphins into contact with the meshes and greatly reduces available surface area.

Chainline (leadline): This is a section of chain that runs the length of the bottom of the net. It is attached to the selvage on the lower edge of the bottom strips of webbing and provides the weight necessary to sink the webbing.

Chute: This is a trapezoidal section of webbing with equilateral sides. It is located atop the apron, but below the corkline. It further optimizes the ramp-formation characteristics of the apron.

Collapse: This is a situation where the corkline comes together, restricting the dolphins' access to the surface. Severe collapse, involving large portions of the net, can result in high dolphin kills. The timely use of speedboats pulling on towing bridles has proven to be an effective measure in reducing the incidence of collapse.

Downhauls (downhaul gate): For this application, a series of rope bridles is attached to the seine's corkline, each attached to a vertical line leading to an anchor point on the webbing directly below. Shortening the vertical line causes the corkline at the bridle above to submerge during the pursing operation to permit dolphin release.

Encirclement: This refers to the stage of the set where the target (either dolphins and tuna, "schoolfish" tuna, or log-associated fish) is surrounded by the net or a combination of the net and towline.

Entanglement: This refers to dolphins being physically stuck in the webbing of the net (or the corkline) by a part of their body such as beak, flippers, flukes, or dorsal fin.

Entrapment: This refers to a situation within the seine where the dolphins are forced into contact with the webbing due to collapse or canopy formation.

Fine mesh: This term is typically used to specify 1¼-inch stretched mesh webbing.

Hand holds: On the purse-seine corkline, spaces between adjacent floats at regular intervals (about 1 fathom) where the webbing is not laced to the corkline. These facilitate the orderly stacking of the corkline during net retrieval but also provide openings where dolphins can become entangled.

Hang-in: This refers to the systematic attachment of webbing to a fixed shorter length of bordering line or chain, usually (in purse seines) in the horizontal plane, to allow the meshes to open vertically (hang) without deforming the bordering line.

Medina panel: This is a 2-inch mesh safety panel that is placed in the net to reduce dolphin entanglement during backdown. Generally one strip deep, it surrounds the apex of the backdown channel, the area where dolphins are most likely to come into contact with the net.

Ortza: This refers to either of the ends of the purse seine which are reinforced. The typical seine net tapers up gradually from the maximum depth to the pointed, wing-like ortzas.

Purse cable: This cable runs through the purse rings, which are connected to the chainline by the bridles. By attaching both ends of this cable to the winch, the rings may be gathered and lifted to the boat. This closes the bottom of the net and precludes subsurface escape of fish.

Purse rings: The rings are attached to the bridles and are gathered by the purse cable. The use of rings permits the pulling and lifting force of the winch to be equally distributed along the chainline during pursing.

Pursing: The process of gathering and lifting the bottom of the net.

Reversed bunchlines: These are ropes that run through small rings which are attached to the corkline of the seine. At one end they are secured to the corkline; a small float is attached to the other end. These lines are 20-50 fathoms long and are arranged so the floats of adjacent bunchlines are close together (1 fathom). A speedboat can secure both end-floats of these lines and, by pulling them away from the net, effectively hold the net, thereby preventing collapse in that area.

Roll-net (net roll): After the net has been pursed, the towing or stern end is led through the power block. The power block begins turning and lifting the net out of the water onto the seiner, where it is methodically stacked for the next set. The net is rolled from the stern ortza until the catch is compressed due to the diminishing underwater volume. This results in the catch being rolled into the sack (which is near the bow ortza). In sets involving dolphins, the net is rolled until the amount of net left in the water is proper for backdown. The roll-net process stops, the net is tied down, backdown takes place, and roll-net begins again.

Roll-up: A roll-up is a recurring type of malfunction whereby webbing and cable become tangled and usually results in a delay of the set (described in text above). The period of time needed to remedy the roll-up varies as a function of its severity and can last from a few minutes to several hours. Pursing of the net is slowed drastically or stopped completely. Canopy formation and/or net collapse may occur as a result of the delay if appropriate precautions are not followed.

Sacking up: When the net has been rolled so that the fish are aggregated, a lifting process begins in which the net is pulled over the rail of the seiner. The net is made shallower by this process, and the fish are further confined and trussed up to the surface where brailing can begin. Normally an auxiliary winch and a choker winch are used to hold the load of the fish being sacked up.

Skiff: The skiff is an auxiliary boat carried on the stern of the seiner. It is generally 20-25 feet long and has a beam of 15-18 feet. The skiff is used in three essential components of the set: 1) It holds the bow ortza during the setting or laying out of the net, making it possible to retrieve both ends of the net after encirclement, 2) it is used with a tow rope (generally polypropylene) to pull on the seiner and optimize its position relative to the net, and 3) it is used to sack up the catch, proving necessary flotation for the catch and a platform for the brailing operation.

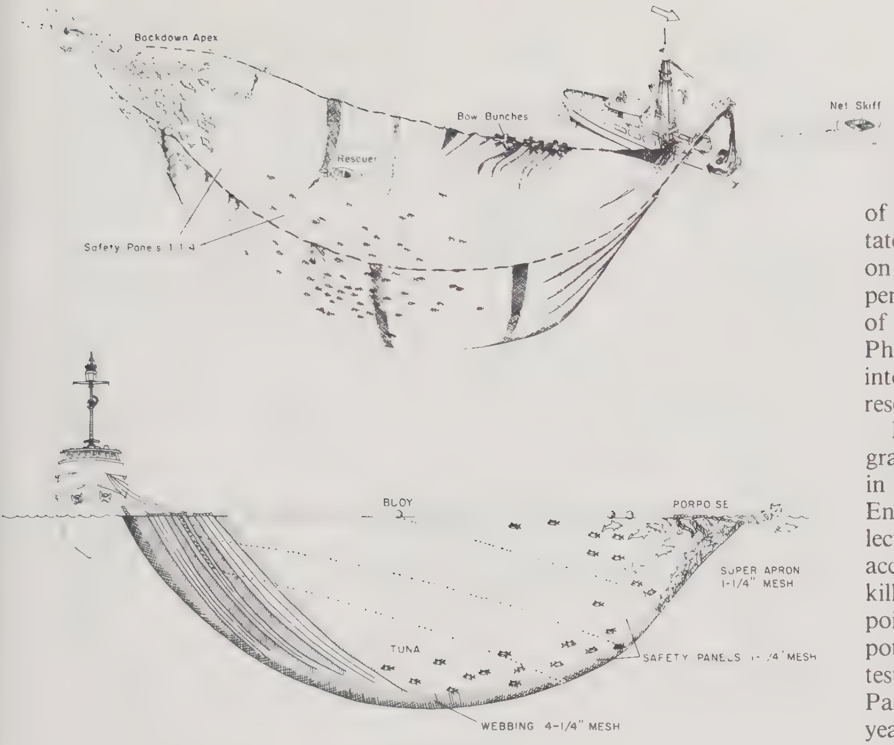
Speedboats: The speedboats carried on seiners are generally 16-18 feet long with a single seat. They are powered by 65-100 horsepower outboard motors and are designed for high-speed, open-ocean operation. Speedboats are used for many different processes in the set: 1) The chase and directing of the dolphin school prior to the set, 2) "patrolling" of the net after encirclement to keep dolphins away from hazard areas, 3) pulling on the net's reverse bunchlines or corkline to prevent collapse, 4) assisting in the process of pulling bow bunches by clearing the bunchlines and tangled corks, and 5) providing a platform for the hand release of dolphins throughout the set, but primarily during and after backdown. Tuna seiners usually use 4-5 speedboats in the course of a dolphin set.

Tie-down point: When a seiner prepares to back down, both ends of the net must be secured in order to withstand the resultant load. Canopy formation is minimized during backdown if the proper amount of net between the outermost bunch and the stern is left in the water. This optimal condition can be attained on every set if the tie-down points are marked. This can be done by painting the proper cork on the corkline (which is secured with the choker winch) and painting marks on the line controlling the outermost bow bunch.

Towline: The towline is attached to the stern ortza and permits retrieval of the ortza in sets where the circle described by the set has a longer circumference than the length of the net.

Winch: This refers to the large hydraulically operated main winch that is used to purse the net. It has three drums; one is used to retrieve towline, and the other two control the ends of the pursing cable.

Zipper: The zipper is a line (usually braided nylon) that runs through small rings which are tied to the net. One end is attached to the corkline at midnet. The other end is attached to the center of the chainline. When the rings have been loaded on the ring stripper, the chainline end of the zipper can be pulled. The midnet corks are pulled to the boat and the net is bisected on a vertical axis. The zipper is used to "cut" the net in sets where the catch is too large to sack up in one bunt without risking a rip and loss of fish. "Cutting" the net with the zipper makes it possible to sack up twice. After making the cut, the fish are divided into two sections of the net, each with a bunt. Part of the catch can be sacked up and brailed aboard from the midnet bunt. After these fish are loaded, this bunt is released. The remaining fish can be rolled to the main bunt and loaded in the normal manner.



Two views of typical purse seines during the backdown procedure.

been conducted. These guidelines specifically recognized the urgent need for research to develop gear and methods to reduce the incidental dolphin-kill rates.

The urgency of this research stemmed from two separate instances. First, biologists and government officials became concerned that the affected dolphin populations were being depleted by the apparent high kill rates. Second, the MMPA provided NMFS with the authority to severely curtail or even close down the U.S. tuna industry to prevent further killing of marine mammals. The Review Committee recognized that a possible result of curtailing or closing the U.S. tuna fishery would be the transfer of vessels to foreign registry. If this were to happen, there would be little likelihood of satisfactorily rectifying the tuna-porpoise problem. Therefore, the Committee recommended that the highest priority should be the development of fishing tactics and gear innovations that would not lessen the effectiveness of the current method of catching tuna. In addition, the innovations would not be too costly and would ultimately permit the harvest of tuna without endangering the dolphin stocks. Through this approach, foreign fleets would adopt these economically feasible innovations, the U.S. tuna fisheries would be maintained, and realistic progress would be made toward marine mammal protection.

The Committee envisioned two mortality reduction research phases. Phase-I was the immediate development and transfer into practice of methods and gear to achieve the lowest possible dolphin kill rates using standard purse seining methods. Phase-II was the research and development of fishing systems that would allow the take of yellowfin tuna without capturing the associated dolphins. The Phase-II work was to be based on behaviorial differences (natural or induced) between the tuna and dolphins and the design of compatible fishing systems to take advantage of those differences.

The need for immediate results in mortality reduction and the limitation of available research funds necessitated the concentration of resources on Phase-I activities. This situation persisted from 1970 through the end of fiscal 1977 when the beginnings of Phase-II research were incorporated into the existing mortality reduction research program.

In general, the NMFS research program has relied on several approaches in finding solutions to the problem. Enough detailed data had been collected by 1974 to allow a reasonably accurate evaluation of the causes of kill in nets. These data helped to pinpoint the major causes of kill so that potential solutions could be devised, tested, and transferred to the fleet. Particularly important in the early years (1970-74) was the search for effective net- and vessel-handling methods and gear refinements employed by a few captains and the dissemination of information on these methods to others in the tuna fleet. In the latter years of the program (1978-81), efforts to quantify and understand the basics of net behavior, especially during backdown (Coe and Sousa, 1972), led to further refinements in the backdown technique and the net design. Data on causes of kill, fleet performance, and net-handling techniques were gathered through both the voluntary observer program (1971-75) and the subsequent mandatory observer program (1976 through 1982) (NMFS, 1975). Experimental gear and methods were tested and modified at sea aboard tuna vessels, including a vessel that was donated by the tuna industry for 1 year (the 1978 "Dedicated Vessel" Program).

Table 2 lists all NMFS charter cruises which conducted mortality-reduction studies during the decade. Technology transfer and dissemination of information on improved mortality-reduction methods were accomplished through the observer program, formal presentations to industry groups, direct waterfront contacts, extension services to the fleet, distribution of published literature, and contact with the Industry's Expert Skippers' Panel (Federal Register, 1977). Regulatory and enforcement regimes established under the MMPA and managed by the NMFS Southwest Regional Office (beginning in 1976) also assisted in the incorporation within the fleet of a wide range of gear and procedures for mortality-reduction.

The total annual dolphin mortality in the U.S. fishery was estimated to be 315,000 in 1970 (footnote 2); by 1980 it had been reduced to an estimated 16,900[3] (Allen and Goldsmith, 1982). These results stem not only from the application of research results, but also from extremely complex social, economic, and legal changes and processes affected through the efforts of many people in both the private and public sectors. In its direct research efforts on mortality-reduction methods and gear, NMFS alone has spent 2.4 million dollars, fielded 3,100 man-days at sea, and employed about 60 temporary and permanent employees. Because of the complex nature of the overall societal effort, the contribution of research to the reduction in total annual dolphin mortality is difficult to estimate.

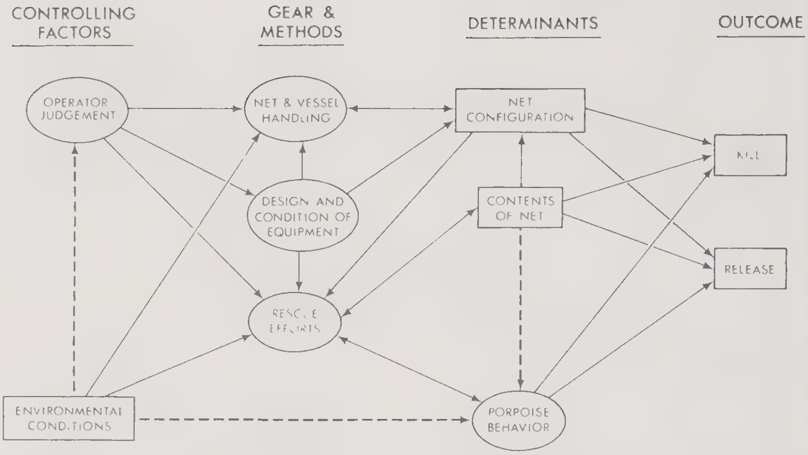


Figure 1.—A generalized schematic showing the operational interrelationships among factors controlling the use of gear and methods to influence the determinants of successful dolphin release from a tuna purse seine. Ovals indicate areas of NMFS applied research and education efforts. Broken lines between blocks indicate uncertainty in the nature of the relationship.

Table 2.—NMFS charter cruises with mortality reduction objectives.

NMFS cruise no.	Vessel	Dates	Cruise leader
	AVR *Miss Behavior*[1]	15 June -20 June 1970	W. F. Perrin
	RV *Cromwell*[1]	3 Sept. - 4 Sept. 1970	W. F. Perrin
	Conquest	21 Dec. -22 Dec. 1970	W. F. Perrin
11	*San Juan*	14 May -15 May 1971	W. F. Perrin
12	*Westport*	7 Sept. - 8 Sept. 1971	W. F. Perrin
13	*Queen Mary*	16 Nov. -17 Dec. 1971	W. E. Evans
26	*Independence*	27 Sept. -29 Oct. 1972	R. L. McNeely
27	*Independence*	11 Dec. -17 Dec. 1972	R. L. McNeely
28	*Independence*	1 Jan. -13 Feb. 1973	F. Wathne
51	*John F. Kennedy*	23 May - 5 June 1973	R. L. McNeely
52	*Trinidad*	16 Oct. -11 Nov. 1973	R. L. McNeely
53	*John F. Kennedy*	10 Nov. -15 Dec. 1973	J. Jurkovich
96	*South Pacific*	28 Oct. - 1 Dec. 1974	R. L. McNeely
97	*J. M. Martinac*	30 Oct. -21 Dec. 1974	D. J. Twohig
131	*South Pacific*	3 July -25 Aug. 1975	F. M. Ralston
132	*Bold Contender*	28 Sept. - 4 Dec. 1975	R. L. McNeely
133	*Eastern Pacific*	29 Sept. - 6 Dec. 1975	J. Jurkovich
207	*David Starr Jordan*[1]	5 Oct. -18 Nov. 1976	D. B. Holts
208	*Elizabeth C. J.*	11 Oct. - 9 Dec. 1976	W. F. Perrin, J. M. Coe
265	*Margaret L.*	19 May -11 Sept. 1977	R. W. McLain
328	*Margaret L.*	27 Oct. -22 Dec. 1977	J. M. Coe
329	*Marla Marie*	2 Nov. -25 Dec. 1977	C. B. Peters
375	*Queen Mary*	26 Jan. -16 March 1978	D. B. Holts
395	*Queen Mary*	17 Apr. - 5 June 1978	J. M. Coe
411	*Queen Mary*	22 June -18 Aug. 1978	F. T. Awbrey, D. A. Bratten
434	*Queen Mary*	12 Sept. -31 Oct. 1978	J. E. Powers
451	*Queen Mary*	11 Nov. - 9 Dec. 1978	D. B. Holts
517	*Cabrillo*	19 May -19 July 1979	G. L. Anderson
552	*Cabrillo*	18 Aug. - 7 Oct. 1979	M. Deerman
565	*Maria C. J.*	17 Sept. -22 Nov. 1979	J. M. Coe
658	*Maria C. J.*	22 Sept. -28 Dec. 1980	J. M. Coe

[1] NMFS research vessel.

The Nature of the Dolphin Problem

Operational Complexity.

Ten years of research have clearly shown that the problem of the incidental dolphin kill is multifaceted and not amenable to "key-discovery" solutions. Aside from occasional shark attacks and encounters with vessel power equipment (speedboats, powerblock, net skiff, brailer, etc.), death of dolphins by suffocation is the rule. Dolphins are killed when confined by the net in such a way that they are unable to rise to the surface to breathe. The animals are either entangled individually in the meshes or are entrapped singly or in groups by folds or "canopies" of net webbing. The probability that animals will become entangled or entrapped depends upon the configuration of the net, the number of dolphins and amount of tuna captured in the net, the behavior of the captured dolphins, the skill of the vessel operator, and the condition of the net and equipment.

Figure 1 is a simplified scheme showing the relationships between circumstances and processes which affect the kill and release of dolphins.

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[3] Estimate includes 5 percent upward adjustment for seriously injured dolphins assumed to have died after release.

Almost every block in Figure 1 represents from three to several dozen components that interact within the block, and with many of the components of the other blocks. Although a complete expansion of this diagram to show all of the known interactions at each level would yield a tangled mass of blocks and arrows, it would serve to illustrate the true complexity of the problem and the degree of skill and attention required of an operator to successfully negotiate sets on dolphins day after day. The estimated annual mortality figures shown in Figure 2 and Table 3 illustrate the effectiveness of the U.S. regulations on gear and methods imposed on operators in 1976, 1977, and 1978, and demonstrate the operators' ability and willingness to incorporate the regulations into their operations. Table 4 indicates a general decrease in the percentage of disaster sets—sets in which a kill of 16 or more dolphins occurred. One would expect to see occasional sets with high kills even from captains with otherwise excellent performance records since environmental conditions, most dolphin behavior, and certain equipment failures cannot be controlled. The number of disaster sets fell to less than 3 percent of all observed sets in 1980. Under the present level of technology, further significant reductions in this percentage appear remote.

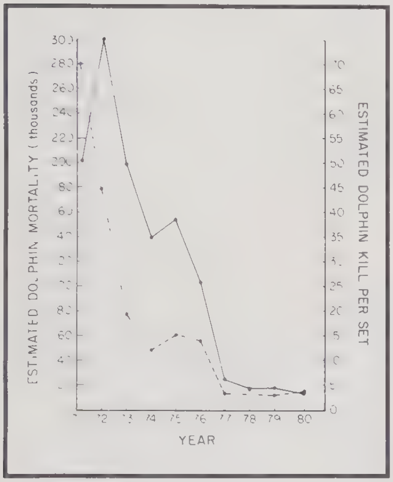

Figure 2.—Estimated annual dolphin mortality (solid line) and kill-per-set (broken line) by the U.S. tuna purse seine fleet.

Pinpointing Causes of Kill

The essential information on specific causes of dolphin mortality and the magnitude of the contribution of each cause was gathered in a variety of ways. In the early years of the program, research directions were based primarily on the field observations of the sea-going staff and on reports from vessel captains. Much of this information was never recorded except in the minds of the researchers because the urgency of the work precluded preparation of lengthy official documents and reports. As the sophistication of the whole "tuna-porpoise" program increased, placing observer records into computers made it possible to store and recover more data related to causes of mortality and fleet performance. Since 1976-77, this data-management capability has

Table 3.—Summary statistics of dolphin sets from NMFS observer trips, 1971-80. Numbers in parentheses are sample sizes.

Statistic	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
1. Total number of dolphin sets	51	273	705	993	948	754	3,408	1,811	2,036	1,007
2. Number of pure spotted-dolphin sets	23	117	302	425	361	255	1,093	931	1,015	587
3. Number of pure spinner-dolphin sets	0	0	17	15	11	9	14	8	7	6
4. Number of mixed spotted and spinner sets	25	132	279	365	412	399	756	680	503	257
5. Number of common-dolphin sets	2	23	105	142	96	55	10	4	7	1
6. Number of others and unidentified dolphin sets	1	1	2	46	68	36	1,535	188	504	156
7. Average tons of yellowfin per set	18(48)	20(272)	14(705)	11(993)	13(948)	13(754)	12(3,408)	11(1,811)	11(2,035)	10(1,006)
8. Average number of dolphins caught per set	219(48)	486(245)	378(705)	355(980)	634(947)	816(720)	813(3,107)	821(1,612)	658(1,797)	643(905)
9. Average dolphin school size per set[1]	298(48)	1,007(239)	907(703)	1,163(866)	1,216(945)	1,419(734)	1,656(3,205)	1,446(1,669)	1,170(1,870)	1,054(935)
10. Average dolphin kill per set	70(48)	43(272)	19(705)	12(993)	16(947)	14(754)	3(3,408)	4(1,809)	3(2,034)	4(1,006)
11. Average dolphin kill per ton of yellowfin tuna	3.8	2.2	1.3	1.1	1.3	1.1(754)	0.2(3,408)	0.4(1,809)	0.2(2,033)	0.3(1,006)
12. Percent dolphins killed of dolphins caught	31.9	8.9	4.9	3.4	2.5	1.8(720)	0.4(3,107)	0.5(1,611)	0.3(1,797)	1.6(904)
13. Percent of school captured[1]	73.5	48.3	41.7	30.5	52.2	57.4(719)	49.6(2,984)	57.5(1,540)	58.3(1,730)	63.1(885)
14. Percent of school killed[1]	23.5	4.3	2.1	1.0	1.3	1.0(734)	0.2(3,205)	0.3(1,667)	0.2(1,868)	0.4(934)
15. Percent of sets catching yellowfin tuna	92(48)	89(273)	82(705)	74(993)	82(948)	83.3(754)	84.7(3,408)	85.3(1,811)	87.3(2,035)	91.3(1,006)
16. Percent of sets catching dolphins	100(48)	91(273)	86(705)	83(993)	91(947)	91.4(720)	95.5(3,107)	97.4(1,612)	97.2(1,797)	99.3(905)
17. Percent of sets catching dolphins with zero killed	2(48)	12(248)	18(601)	22(827)	24(863)	30.4(658)	56.5(2,968)	58.4(1,569)	71.4(1,746)	67.5(898)

[1] Estimates generally have a low precision.

Table 4.—Summary statistics of sets with dolphin kill greater than 16, from NMFS-observed trips. Number of dolphins killed.

Year	Number of sets (%)	Total kill	Backdown canopies: Bow	Backdown canopies: Stern	Backdown canopies: Other	Backdown canopies: Total	Pre-B.D. net collapse	B.D. channel collapse	Malfunction mortalities	All other causes	Unknown
1977	135(4.0)	5,277	749	1,539	774	3,062	440	346	329	339	780
1978	73(4.6)	4,932	478	486	872	1,836	1,897	338	397	243	221
1979	54(3.5)	2,879	960	173	43	1,176	284	326	84	925	84
1980	30(2.9)	2,647	106	206	220	532	29	1,504	303	140	139
Total	292(3.9)	15,735	2,293	2,404	1,909	6,606	2,650	2,514	1,113	1,647	1,224
Percent of total kill		100	15	15	12	42	17	16	7	10	8

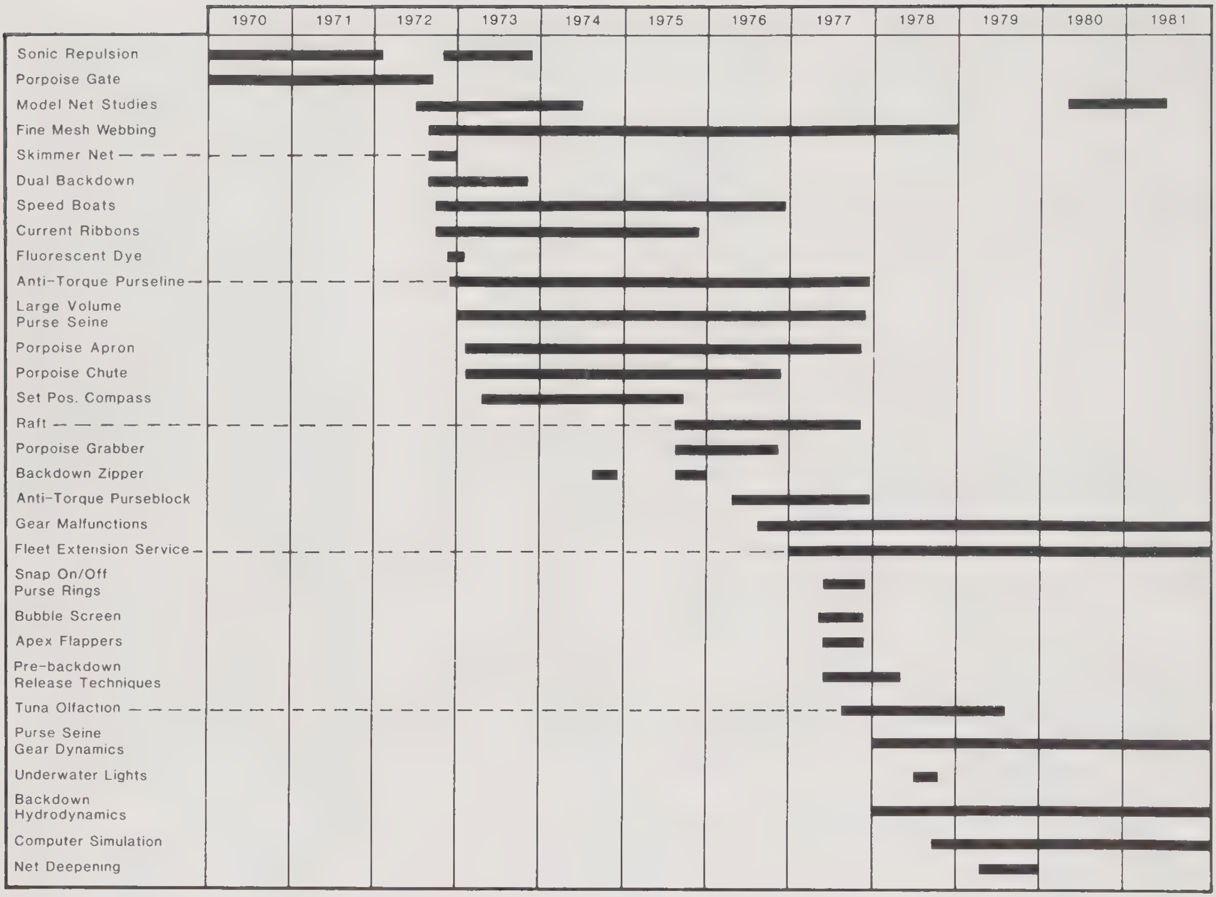

Figure 3.—Areas of NMFS dolphin mortality reduction research since 1970, by subject areas.

allowed analyses that assess the performance of experimental gear and techniques and that allow tracking of the major causes of dolphin kill. Table 4 shows the primary causes of kill for disaster sets from 1977 through 1980. The primary causes are related to net configuration (i.e., backdown canopies, prebackdown net collapse, backdown channel collapse). Most of the malfunction-related kill is also due to resultant net-configuration problems. An example of an "other" cause of mortality is when the dolphins are "sacked-up" in the bunt with the tuna and suffocated. The unknown causes of kill are, for the most part, related to the behavior of the captured dolphins.

Specific Research Efforts

Shown in Figure 1 are the areas in which NMFS has focused its research. Net and vessel handling, so as to minimize net-configuration problems, was of primary importance along with the development and improvement of effective rescue and release techniques. Some effort has gone into the search for methods of eliciting differential responses of tuna and dolphins that could be employed in separating them before or during a set. In this section, the specific areas of research are discussed. They have been categorized according to the functional areas presented in Figure 1. There is a significant overlap among these categories because of the multidimensional nature of the problem. Research projects that apply to two or more categories are grouped into the category most closely related to the original intent of the project. Figure 3 lists the specific areas of research chronologically and shows their approximate duration during the NMFS mortality-reduction program.

Net and Vessel Handling

Table 4 indicates that net configuration has a major influence on dolphin mortality. Chief among the various configuration problems is prebackdown net collapse, which can be caused by strong currents, changes in wind direction and strength, major equipment malfunction, failure of the captain to orient the set properly with the wind, or any combination of these problems. Regardless of the cause of prebackdown net collapse, the outcome is the same; that is, a substantial portion of the captured dolphin school will be killed and the tuna may be lost as well. Because the fishery will, at times, involve setting despite adverse conditions and because equipment may occasionally fail, the development of a means to prevent net collapse rather than remove the causes was essential.

Speedboats to Prevent Net Collapse

Beginning in late 1972, experiments on the use of speedboats to prevent net collapse were initiated. Since most tuna seiners carried four or five speedboats for herding dolphins, the means for towing on the net were readily available. During the chartered cruises of the M/V *Trinidad* (1973), the M/V *John F. Kennedy* (1973), the M/V *South Pacific* (1974), and the M/V *Bold Contender* (1975), the methods and the practicability of using up to three speedboats to tow on the net to prevent net collapse under most conditions were proven[4,5].

Tests during commercial fishing operations showed that the temporary crew reduction on deck while speedboats were towing did not cause a marked increase in the duration of the set, especially when the alternative of dealing with large numbers of dead dolphins was considered. However, to avoid reducing the deck crew during a set, most captains became more attentive to their methods of setting in order to reduce the likelihood of net collapse. A substantial portion of the reduction in observed kill-per-set was due to increased awareness on the part of the captains. The 1976 regulations required at least two speedboats to be in the water during every set on dolphins and that they be crewed and prepared to tow on the net should it be necessary before the start of backdown. Since the need to tow on the net to prevent imminent collapse was infrequent if captains were careful, this regulation was considered a nuisance and was ignored by many captains.

Optimizing Set Orientation

While the use of speedboats was being developed, devices to provide more information to the captain on the direction of the current and the orientation of the set relative to the wind and current were examined. With this information, the captain could select the optimal set orientation to minimize the potential for net collapse. A current-direction indicator consisting of a roll of approximately 100 m of surveyor's tape with a weight on one end and a float on the other was tested on the cruises of the M/V *John F. Kennedy* (1973), the M/V *Trinidad* (1973), the M/V *J. M. Martinac* (1974), the M/V *South Pacific* (1974), and the M/V *Bold Contender* (1975).

Concurrently, a multibezel compass was devised that allowed the captain to set the bezels for wind and current direction (from the current-direction indicator) and to determine the direction in which to initiate the set that best balanced those forces on the net. The current indicators were found to be unreliable because they only indicated surface-current direction while it is the difference in magnitude and direction of surface and subsurface currents that affects the net.

The multibezel compass provided the correct information to properly orient a set. However, the business of orchestrating the chase and controlling the activities on board the seiners generally kept captains too busy to use this tool. Since the current indicators were not always reliable, and the multibezel compass only showed the correct orientation to the wind, which was available to the captain from direct observation, there was no need for the compass. This line of experimentation was therefore dropped.

Preventing Roll-ups

Most purse seine sets are not likely to result in a collapsed net if the net is retrieved without much delay. A common delay in purse seining is the roll-up in which the purse cable, leadline, and webbing become wrapped around one another, usually in both directions of rotation, such that they lock against each other. When a severe roll-up occurs, the net cannot be pursed until the roll-up is cleared. The delay can result in net collapse if speedboats are not used to hold the net open.

NMFS began studying the cause of roll-ups in late 1972 and discovered that roll-ups are caused by the purse cable rotating as tension is increased or decreased. Standard wire rope used for purselines is analogous to a long spring that, when stretched, creates torque along its length. When tension is applied, the cable rotates in one direction, and when tension is relieved, the cable rotates in the opposite direction. If, when setting the net, the leadline or webbing comes into contact with the rotating purse cable and is snagged, a roll-up results. Roll-ups occur occasionally on every vessel in the fleet.

In 1973, antitorque purselines were constructed and tested on chartered cruises of the M/V *John F. Kennedy* and the M/V *Trinidad*. These purselines were constructed of torque-balanced wire rope, which allows virtually no tension-induced rotation to occur because of the opposing lay of its major and minor component strands. The tests showed that the antitorque purseline worked. Beginning in 1974, NMFS supplied the cable to vessels that were experiencing a high frequency of roll-up sets. Roll-ups, however, still occurred on these vessels but less frequently. The fishermen also encountered a problem with the press fittings used to form eyes at the end of the cable. When the press fittings passed over the purse blocks they eventually cracked and required repair. A special splicing technique to form the eyes was developed. However, the fishermen did not completely accept this remedy, and by

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[4] Everett, J., J. E. Powers, R. McNeely, J. M. Coe, and R. Butler. 1976. The use of speedboats in reducing incidental porpoise mortality in tuna purse seining. U.S. Dep. Commer., NOAA, NMFS, SWFC Admin. Rep. LJ-76-35, La Jolla, Calif., 29 p.

[5] McNeely, R. L., and D. B. Holts. 1977. Methods of reducing porpoise mortality in the yellowfin purse seine fishery. U.S. Dep. Commer., NOAA, NMFS, SWFC Admin. Rep. LJ-77-13, La Jolla, Calif., 19 p.

1976 most of the vessels that were experimenting with antitorque purselines replaced them with conventional purselines.

That roll-ups still occurred with the antitorque purseline indicates that the cable is not rotation free. The torque-balanced cable has a much longer, more open lay than conventional cable, and when passed over standard purse blocks under tension it has a tendency to flatten out. This "unlaying" of antitorque cable on the sheave of the purse blocks artifically induces torque (and rotation) into the purselines. To correct this problem, special purse blocks were designed with a 20-inch pitch diameter that were counterbalanced so the cable would always ride in the center of the sheave and not flatten out. A system of antitorque purseline and counterbalanced purse block was tested during three cruises aboard one of the more roll-up prone seiners. The results were inconclusive[6,7] and the research was terminated. To date, the antitorque system has not been further developed or incorporated into the fleet.

Quick Release Purse Rings

To remove and reattach purse rings easily during pursing has potential for increasing the speed with which the net can be retrieved when a malfunction occurs. A fisherman, Raphael Guillen, invented a snap link for this purpose in 1976. The NMFS tested this device during the chartered cruise of the M/V *Margaret L.* in 1977. The snap links were found to be useful in reducing delays in net retrieval and the device was recommended to the fleet.

Optimizing the Backdown-Channel Configuration

The most delicate and also most important net- and vessel-handling technique in a purse seine operation involving dolphins is backdown. A large part of the dolphin mortality occurs during backdown (Table 4). By the end of 1977, considerable progress had been made in solving the problem of prebackdown net collapse, and biologists had begun to understand the dynamic processes governing breakdown-related dolphin mortality.

A diving program was established, a model-net study program was initiated, and instruments for recording depth, depth/time relationships, net and vessel speed differentials, and relative changes in enclosed surface area were assembled. Cruises of the M/V *Queen Mary* in 1978 and the M/V *Maria C.J.* in 1979 and 1980 were designed to collect information on net behavior during breakdown. Observations from those cruises resulted in recommendations for an improved mid-net zipper design (Holts, 1980), more precise net tie-down locations on the net for optimal backdown-channel configuration, and instructions for determining causes and remedies for poor backdown performance (Coe et al., In press). This work also served to identify some previously unknown features of backdown dynamics.

Net-Depth Effects

With the development of improved methods for assessing the physical performance of a purse seine, efforts to quantify and demonstrate the positive effects of increased net depth were carried out. With bathykymographs and a systematic method for approximating net-enclosed surface area, an experiment was run aboard the M/V *Cabrillo* in 1979. For the experiment, the *Cabrillo's* net was deepened by two standard strips tapered at each end and inserted at the leadline. The average fishing depth of the net was increased by 17.3 m (9.4 fm) using six bales[8] of webbing. Net-enclosed surface area was increased by an average of 11.5 percent which gave the dolphins more room to move both before and during backdown. This also increased the time for the net to collapse. As a result of this experiment, specific performance data were collected to support the long-standing NMFS recommendation (footnote 5) that nets used on dolphin schools should be deepened whenever possible.

Miscellaneous Techniques

Many simple methods of employing standard vessel- and net-handling gear to minimize net configuration problems were recorded and shared with captains in the fleet. Most of these methods were obvious and effective but were not necessarily widely known. For example, in a normal set the captain has at his disposal the use of the net skiff, the bowthruster, and the main engine to prevent net collapse and to position the vessel in order to effect a smooth transition into backdown. Coe et al. (In press) discussed these techniques in detail.

Dolphin Handling Methods and Gear

While research on net- and vessel-handling techniques sought to prevent situations that directly endangered dolphins confined in the net, research on dolphin handling methods and gear sought ways to release dolphins efficiently from the net. Again, many of the effective methods for dolphin handling were practiced by the fishermen before this research program was begun, though many either were not widely used or were not being employed to their maximum effectiveness. Obvious examples are the backdown maneuver and the Medina Panel (see Glossary: Table 1).

Alternatives to Backdown

One of the earliest and most commonly suggested solutions to the tuna-porpoise problem was a gate built into the net that could be opened to allow the dolphins to swim away. A porpoise gate was built and tested aboard NMFS research vessels in 1970 and the M/V *Westport* and M/V *San Juan* in 1971. The gate (an inflatable/deflatable tube replacing a section of corkline) performed as designed. It sank rapidly to provide a controllable 15 m wide by 4.5 m deep opening. The dolphins, however, would not take advantage of the opening despite being herded with skiffs and a false corkline with evenly

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[6] Coe, J. M., and D. A. Bratten. 1978. Cruise Report: M/V *Margaret L*, October 27-December 22, 1977. NMFS Southwest Fish. Cent., La Jolla, Calif. Unpubl. rep., 9 p.

[7] McLain, R. W., D. A. Bratten, and J. M. Coe. 1977. Cruise Report: M/V *Margaret L.*, May 19 to Sept. 11, 1977. NMFS Southwest Fish. Cent., La Jolla, Calif., Unpubl. rep., 8 p.

[8] 100 meshes deep × 100 fathoms long, stretched mesh.

spaced drop lines. White noise (randomly generated sounds of equal energy) and killer-whale sounds were also used to herd the dolphins to the opening without success. These results illustrated a fundamental behavior of dolphins: The dolphins are more afraid of the net than of anything within it. To release them from the net requires some active process that literally pulls the net out from under them. Although this principle was recognized early on, several alternative methods for release were also considered in the early and mid 1970's.

Dual Purselines

The first alternative method was based on the hypothesis that early in a set there is a distinct vertical separation of tuna and dolphins (the dolphins at or near the surface and the tuna well beneath). It was proposed that a secondary purseline be installed at mid-depth, running the length of the net, that could be pulled at the same time as the standard purseline. Thus the pursed net would be divided into upper (dolphins) and lower (tuna) compartments (footnote 2). The corkline could then be opened with a zipper arrangement, and the dolphins either would swim out or be forced out by pulling the net from under them. A model net was built in mid-1972 to test the mechanics of this concept. However, further work on this was abandoned when underwater observations made aboard the M/V *Independence* in late 1972 showed that there was no consistent spatial or temporal separation of tuna from dolphins in the net.

Skimmer Net

In late 1972 the idea of using a lampara-type skimmer net was tested to see if the dolphins could be quickly gathered together and dumped over the corkline soon after pursing was completed. The M/V *Independence* was chartered for tests off southern California. The tests showed that the concept did not work because: 1) Most of the dolphins easily avoided the skimmer net, 2) dolphins that were herded to the corkline were trapped there and could not be easily released, and 3) speedboats did not have enough power to pull the skimmer net effectively.

The Dual Backdown

NMFS observations indicated that a number of dolphins were often left alive in the net after backdown. Afraid of losing the tuna, the captains discontinued backdown before all the dolphins were released. As a possible solution to this problem, a dual backdown system was conceived in 1973 and tested using model nets aboard a chartered salmon seiner and the tuna seiners M/V *John F. Kennedy* (May 1973) and M/V *Trinidad* (October 1973).

The dual backdown principle involved the development of a net configuration with two backdown channels of approximately equal size adjacent to each other, with a controllable passage between them. Tuna normally cruise up and back in the channel during backdown, so that they might be directed through a passage into the second channel and held there without risk of escape while all of the dolphins were released from the first channel. In practice, the dual channels were difficult to form without collapsing them, and the tuna were never effectively transferred to the second channel. The idea was therefore abandoned as impractical.

Small Mesh Safety Panels

Harold Medina observed that the standard mesh size (4¼-inch stretched mesh) for tuna seines was much too large to prevent the entanglement of dolphin snouts and flippers. In 1970 he installed a strip of 2-inch stretched mesh webbing at the backdown apex of his net and noted good results. Data collected by NMFS observers in 1971 and 1972 (footnote 2) from vessels with and without the 2-inch panel confirmed Medina's results, showing lower mortality rates for vessels with the smaller mesh panel. A great deal of subsequent industry and NMFS research effort from 1972 through 1977 went into extending Medina's concept and developing better safety panels for the backdown channel, since backdown literally forces the dolphins into contact with the net while effecting their release.

The single-strip, 2-inch mesh Medina Panel was rapidly incorporated into nets of the U.S. fleet, and by 1974 nearly all nets had it. Some captains chose to use two strips of 2-inch mesh of varying lengths for their backdown apex. In 1973 experts questioned whether the 2-inch mesh was the ideal size to prevent entanglement. NMFS conducted a series of experiments to determine the mesh size that was most effective in preventing entanglement of beaks and flippers (Barham et al., 1977) and found that 1¼-inch stretched mesh was most appropriate. Accumulated observations of where dolphins became entangled in the channel were used to establish NMFS specifications for the placement of 1¼-inch mesh safety panels, which replaced the 2-inch mesh Medina Panels.

In 1973, NMFS designed and built a large volume net that was 17 strips deep. The net's backdown area was protected by a safety panel that was made up of three standard-depth strips of 1½-inch stretched mesh webbing. The large-volume net was tested on cruises in late 1973 (M/V *John F. Kennedy*) and 1975 (M/V *South Pacific*) with encouraging results. Further refinements in safety-panel design were investigated during the 1976 fishing season, when 20 volunteer vessels were equipped with 1¼-inch mesh safety panels either with or without an apron-chute appendage (see below). The kill rate for these vessels were markedly lower than those for vessels with a regular net[9]. In 1977, all vessels were required to install two strips, each 340 meshes deep, of 1¼-inch mesh webbing 180 fathoms in length, starting within the second outermost bow-corkline bunch and running sternward. The industry accepted this modification as a progressive change, and, although there were some webbing supply problems, most vessels were in compliance by the end of 1977. The reduction in kill rate from 14 animals per set in 1976 to 3 animals per set in 1977

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[9] Coe, J. M., and J. DeBeer. 1977. Results of the 1976 twenty-vessel test of two fine mesh systems to reduce incidental porpoise mortality in tuna purse seining. Unpubl. manuscr. on file at NMFS Southwest Fish. Cent., La Jolla, Calif., 75 p.

(Table 3) was, in our view, largely the result of this change in net design.

Preventing Backdown Canopies

While collecting data on the backdown procedure, biologists observed that net canopies made dolphin release more difficult and contributed to dolphin mortality. Surface net canopies entrap dolphins and prevent them from drifting or swimming to the apex of the backdown channel to be released from the net. Because of the canopies, up to 20 animals were occasionally left in the net after backdown.

To eliminate surface canopies, the slack webbing near the surface of the backdown channel needs to be redistributed to optimize the amount of net in the water. In the fall of 1974 a tapered, trapezoidally-shaped section of 2-inch mesh webbing called the "apron" was installed in the net of the chartered vessel M/V *South Pacific*. The apron was inserted between the corkline and the upper edge of the safety panel, with its short side up, and centered at the backdown apex. This installation required tiedown to be at the same place for each set. On this cruise, the apron was tested and judged effective in reducing surface canopies in the backdown channel.

A number of vessels volunteered to test aprons during the 1975 fishing season and had mixed results and opinions[10]. A similar 1¼-inch mesh apron with a more sharply tapered extension piece mounted at its top center (called the "chute") was installed with a 1¼-inch mesh safety panel in the net of the M/V *Bold Contender* in the fall of 1975. Results with this net design were extremely encouraging, producing kill rates well below the 1975 fleet average. The "Bold Contender System," as the apron-chute complex came to be known, was tested on 10 vessels and compared with 10 vessels using only the two-strip, 1¼-inch mesh safety panel. This test ran the entire year of 1976. When the results were analyzed, both systems were found to produce significantly lower kill rates than did conventional gear, with the Bold Contender System slightly better than the safety panel alone (footnote 9 and SWFC[11]).

During this 20-vessel test, some simple problems in handling the Bold Contender System were identified. To deal with these problems, the chute was trimmed down so that the remaining "super apron" was a long, low triangle with its apex coinciding with the desired backdown channel apex. This modification seemed to eliminate the handling problems. The net design was adopted voluntarily by a number of vessels in the fleet, based on the results of the fall 1976 chartered cruise of the M/V *Elizabeth C. J.* The super apron became mandatory by regulation beginning in 1978.

The Backdown Zipper System

At the same time that the apron was developed, biologists designed a method to reduce the risk of loss of tuna during backdown. A series of 3-inch steel rings were lashed to the net in the backdown area in a way that allowed a rope to be strung through them. The rope, when pulled, pinched the channel shut near the apex. The idea was to back down until all the dolphins were at the apex and the tuna had moved toward the boat, and then to pull this backdown zipper separating the dolphins and tuna.

During the charters of the M/V *South Pacific* (1974) and the M/V *Bold Contender* (1975), the mechanics of the zipper proved sound, but the dolphins were not always on the apex side. In addition, the zipping action caused the apex end of the backdown channel to become shallow and to collapse. The animals became entrapped and were not easily released. The zipper idea was therefore rejected. As an alternative, the apron was refined so that it produced a sloping apex floor that tended to turn the fish away from the release area and thereby reduce the loss of fish during backdown.

Releasing Dolphins by Hand

In considering ways to increase the number of sets with no dolphins killed, it was recognized that backdown alone rarely got every animal out of the net and that some efficient form of hand-release of individual animals was needed. Several rescue techniques for hand-release were already in use in the fleet prior to NMFS involvement. These were: 1) Rescuers in speedboats released animals at the surface and next to the corkline, 2) rescuers dove and swam in the net to catch and release both entangled and free-swimming dolphins, and 3) from the speedboats and the net skiff, rescuers used gaffs to guide dolphins over the corkline. Rescue from speedboats was inefficient because of the rescuers' limited reach and lack of mobility. Swimming in the net was fairly efficient, depending on the skills of the rescuer, but dangerous because of potential shark attacks and rescuer entanglement in the net. Gaff wounds are potentially fatal to dolphins, depending on the severity and location of the punctures.

During a cruise aboard the M/V *Gina Karen* in 1974, it was noted that having two persons aboard a speedboad stationed at the backdown apex during backdown increased efficiency of hand-release of dolphins. Analyses of data from the fleet supported this conclusion, and the practice was made a requirement in 1975. During the charter cruises of the M/V *Bold Contender,* the M/V *Elizabeth C. J.,* and the M/V *Margaret L.,* NMFS tested the feasibility of using an inflatable one- or two-man raft as a platform from which rescue could be performed. It was found that, with practice, a single man in the raft could easily maneuver the raft and, with the aid of a face mask and snorkel, rescue dolphins more efficiently than any other method. Furthermore, the raft provided some protection for the rescuer from shark attacks, while the face mask allowed him to see clearly whether there were sharks, billfish, stingrays, or jellyfish in the area where he was working. This raft-rescue technique has been in use by the fleet since 1976. Since hand-release in any form is not without some risk, the regulation is written so that raft use is at the captain's discretion.

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[10] Coe, J. M. 1976. The effectiveness of the porpoise apron in improving the backdown procedure. U.S. Dep. Commer., NOAA, NMFS, SWFC Admin. Rep. LJ-76-38, La Jolla, Calif., 17 p.

[11] SWFC. 1972. Unpubl. manuscr. by SWFC Staff on file at Southwest Fish. Cent., La Jolla, Calif.

While the raft-rescue technique was being tested on the M/V *Bold Contender* and M/V *Elizabeth C. J.*, some dolphins were observed to drop out of the school at the surface and come to rest passively on the floor of the backdown channel for a few minutes before rejoining the school. Without a mask and snorkel, the rescuers were not able to see these passive animals. The animals the rescuers did see were presumed dead. Passive behavior (Coe and Stuntz, 1980) was largely responsible for the unexpected appearance of live dolphins in the net after what had seemed to be a completely successful backdown with all dolphins released. The raft rescuer with a mask and snorkel can see the passive dolphins, signal the captain to continue backdown, and rescue the dolphins as they come to the surface. A regulation requiring the raft rescuer to wear a mask and snorkel also required backdown to continue until all live dolphins were released from the net. We believe that this regulation has contributed to the increased frequency of zero-kill sets after 1976 (Table 3) and the overall reduction in dolphin mortality.

Regulations in 1976 made the use of gaffs or other sharp-pointed instruments on dolphins illegal. When direct hand-release was not feasible (e.g., during sacking-up, after backdown, in the presence of sharks) a long-handled instrument (shepherd crook) for moving and controlling dolphins was needed and NMFS designed, built and distributed a number of different types of shepherd's crooks between 1975 and 1977. Results and opinions varied considerably among the users, but it was clear that in many circumstances the crooks could be effective and the degree of effectiveness depended on the user's effort. Many vessels have carried and made use of the devices.

The Apex Flapper

Behavioral observations made during the development of the raft rescue technique led to studies on altering the structure of the backdown apex to make it easier for the dolphins to leave the net. During backdown, many dolphins come into contact with the net just below the corkline and either swim back into the channel or lie against the webbing and are carried with it. Also, when tuna approach the backdown apex they see the webbing and corkline and usually turn back into the net, even though the corkline may be 3 or 4 feet underwater. It was reasoned that if the apex could be made semipermeable to dolphins and still present a visual barrier to the tuna, a more efficient backdown might result.

The initial and only attempt to design a differentially permeable apex produced the apex flapper system, which consisted of overlapping trapezoidal pieces of 1¼-inch mesh of increasing height placed above the corkline and centered at the backdown apex. A flat spot of about 20 fathoms was cut at the top of the apron (at the backdown apex), most of the floats were removed from the corkline, and the flappers, with floats attached at the top and middle, were laced in along the apex flat spot. This modified apron was tested on the M/V *Margaret L.* in the fall of 1977. Tests showed that too much flotation was left at the corkline, so the flappers tended to float on the surface inhibiting release and rescue at all but the highest backdown speeds. The merits of the apex flapper concept were never fully assessed and the method has not come into use.

The Downhaul Gate

Aboard the first cruise of the dedicated vessel M/V *Queen Mary* in 1978 (DeBeer et al.[12]), a simple system of downhauls in the half-net area that could be adjusted in length to cause the corkline to sink during pursing was rigged for testing. The intent was to create an opening through which dolphins could be driven before the purse rings were brought on board using the downward force on the corkline exerted by the purse winch. Before the test could be conducted, however, the downhaul ropes became tangled in the corkline during setting, and had to be removed.

Other Modifications

A number of additional minor dolphin-rescue modifications pursued during the decade deserve brief mention. During the chartered cruises of the M/V *J. M. Martinac* (1974) and the M/V *South Pacific* (1974), the effectiveness of closing the hand-hold openings and corkline hangings to prevent entry of dolphin beaks and flippers was shown. Regulations to implement this finding were enacted in 1976. Experiments to determine the efficiency of large safety panels and aprons on the smaller vessels in the fleet were run on the M/V *Eastern Pacific* (1975) and the M/V *Marla Marie* (1977) with mixed results.

Evaluating Integrated Net Designs

The means for testing and demonstrating the gear ideas developed by the project ordinarily consisted of simple vessel cruises employing their own net with a specific modification. The high cost of dedicated vessel time and net construction and maintenance prohibited the integration and testing of broad combinations of experimental gear. However, three methods were developed to evaluate multiobjective gear designs: 1) A full-sized net, 2) scale-model nets, and 3) an interactive computer simulation of net behavior.

Large-Volume Net

In the summer of 1973, this prototype net was designed to demonstrate a number of advanced dolphin-saving features as well as advanced fishing technology. Its decreased length:depth ratio and sharply tapered ends increased the enclosed surface area (and volume) when pursed, reducing the probability of net collapse. It was the first net to have three strips of dolphin-safety panel of less than 2-inch mesh (today's nets with aprons effectively have 3⅓-strip safety panels of 1¼-inch mesh). It was also the first net to have handholds and corkline hangings laced shut in the backdown area to prevent entanglement. Lighter than normal twine was employed in the body of the net, which saved material costs and let the net sink and be pursed more rapidly (an idea that has recently been employed by the fleet). Its depth of 17 strips of webbing was 5 or 6 strips deeper than most nets in the fleet at that time (today 15- or 16-strip nets are quite common). Its advanced designs have only recently gained wide acceptance. By 1975 the cost of maintenance and repair of this net was too high and the project was transferred to another Federal agency.

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[12] DeBeer, J., F. Awbrey, D. Holts, and P. Patterson. 1978. Research related to the tuna-porpoise problem: Summary of research results from the first cruise of the dedicated vessel, January 26 to March 16, 1978. U.S. Dep. Commer., NOAA, NMFS, SWFC Admin. Rep. LJ-78-14, La Jolla, Calif., 27 p.

Scale Models

Two scaled-down model nets were built early in the program to study radical changes in fishing procedures and net designs. The first model was a 1:25 scale model of a nine-strip deep net which had a midnet purse line running the entire length. It was used to test the feasibility of double pursing to separate the tuna from the dolphins. These tests showed the concept to be unpractical, saving considerable time and resources in the early period of the program.

A second 1:50 scale model of a newly designed purse seine was constructed in the spring of 1973. This model featured 1) 17 strips to provide greater surface area thus preventing net collapse, and 2) tapered ends to reduce excess webbing and attendant gear malfunctions. This model showed sufficient promise and a full-sized, 17 strip, purse seine (the Large-Volume Net) was built in the fall of that year.

These early tests provided valuable information on purse seine dynamics and were useful in focusing research effort and resources on specific problem areas. They were again used in 1980 (Holts and Coe, 1982) to study the dynamics of both normal and modified backdown procedures as well as various related gear malfunctions.

Computer Simulation Model

There are two principal methods of determining net behavior: Experimental and analytical. The experimental method has the overwhelming advantage of producing tangible and irrefutable results. The disadvantages of the method are numerous: The expense of chartering fishing vessels is great, ocean parameters cannot be controlled and are difficult to measure, and modifying nets is costly.

In direct opposition, the analytical method has the disadvantage that the results are not real and may be challenged. This disadvantage can be eliminated by comparing the results of analysis with experimental measurements. If the analysis is verified by this comparison, the advantages of the second method are realized: Low cost and control of the ocean and net parameters. The key to obtaining these advantages is experimental verification.

From 1978 to 1981 a substantial portion of the funds for the mortality reduction project was spent to research and develop a computer-based, interactive numerical simulation of purse seine behavior and to establish field measurements with which to verify the results of the simulation program. Basic performance parameters such as sinking rates, pursing speed and tension, enclosed area and volume, setting speed, retrieval speed and backdown forces, and net skiff towing force were measured on the dedicated vessel (1978) and charters of the M/V *Maria C. J.* (1979 and 1980).

The computer simulation was developed in three phases under contract and was nearing completion in the fall of 1981. The simulation program was based on a system of differential equations which describe the motion of the net to be simulated. The user defines a sequence of external events (water currents, setting, pursing, etc.) affecting the motion which is to be simulated. The product of a simulation consists of a binary file for graphics display. Ultimately, the simulation was intended to be a broadly flexible tool for computer aided design (CAD) for a variety of fishing systems. This flexibility and accuracy were essential for cost-effective development of fishing systems directed to Phase-I goals. This program was terminated before benchmark runs could be carried out and simulation limits verified. Although the model was not used to solve fishing gear problems, it was used to simulate towed cables (Delmer et al., 1983) and changing and breaking cable systems (Stephens et al., 1982).

Behavioral Research

Throughout the decade, researchers have been trying to identify a key behavioral response by either the dolphins or the tuna that could be used to temporarily break the tuna-porpoise bond. Investigations, therefore, concentrated on mechanisms that could release dolphins from conventional purse seine nets (i.e., Phase-I work) and which might also serve as a basis for the development of alternate fishing systems not involving the capture of dolphin schools (Phase-II).

In their search to find ways to direct or elicit a predictable response (movement in a desired direction), researchers experimented with testing a wide range of acoustical signals on captured dolphins. Killer whale vocalizations to white noise and sounds of dolphins escaping were some of the signals tested. No underwater sound presented to captured dolphins has produced a response potentially useful in improving release efficiency. The first work was done in 1970 on the R/V *Miss Behavior* and the latest and most sophisticated work was done on the dedicated vessel,

Table 5.—Major malfunction categories showing frequency of occurence, severity in terms of percent malfunction-related mortality, and average loss of time for each of the 4 years, 1977-80.

	1977			1978			1979			1980		
Malfunction	Sets f (%)	Kill %	Delay min.	Sets f (%)	Kill %	Delay min.	Sets f (%)	Kill %	Delay min.	Sets f (%)	Kill %	Delay min.
Speedboats	120 (15)	9.1	1.0	78 (21)	2.1	1.2	82 (30)	13.3	1.4	85 (32)	0	8.0
Roll-up	151 (18)	12.3	34.0	59 (15)	11.6	46.7	39 (14)	16.9	53.2	22 (8)	13	57.2
Net tangled in rings	129 (16)	12.8	16.1	42 (11)	28.7	19.3	31 (12)	4.6	15.2	29 (11)	34	26.5
Purse cable	94 (11)	12.5	17.9	27 (7)	15.3	11.9	22 (8)	23.7	16.3	12 (5)	7	22.4
Hydraulic problems	73 (9)	5.0	22.3	44 (12)	4.6	27.7	17 (6)	4.7	18.4	24 (9)	3	26.2
Bow bunches	41 (5)	5.1	5.8	37 (10)	2.0	15.9	22 (8)	5.6	14.9	14 (6)	1	7.7
Skiff	63 (8)	18.1	23.1	35 (9)	7.6	16.3	29 (11)	21.1	17.7	17 (6)	8	13.7
Winch and stripper				12 (3)	1.8	17.8	6 (2)	2.7	41.7	0 (0)	0	0
Other	144 (18)	22.5	20.3	44 (12)	26.1	11.9	23 (9)	7.4	15.8	60 (23)	34	21.3

M/V *Queen Mary* in 1978[12, 13].

Visual stimuli were also tested briefly on a cruise of the M/V *Margaret L.* (fall 1977) and on the dedicated vessel. A bubble screen, created by scattering chunks of dry ice across the backdown channel, was tested in several sets of the M/V *Margaret L.* The bubble screen did not produce a clear, consistent response by the dolphins. Underwater strobe lights and underwater magnesium flares were tested on the M/V *Queen Mary* cruises, both day and night, before and during backdown. These tests also showed that dolphins do not respond to these visual stimuli in any predictable way.

Under contract to NMFS, researchers at the University of Hawaii developed various concentrations of natural chemical extracts of prey species and organic debris to test the response of captured yellowfin tuna to olfactory stimuli[14]. The researchers were able to elicit strong feeding responses in laboratory tuna with these extracts. They hypothesized that by presenting the extract that evoked the strongest response to tuna in the net they could be held stationary while the net was opened to release the dolphins. In field tests aboard the M/V *Queen Mary* in the summer of 1978, these olfactory lures did not produce a strong enough response by the tuna to warrant continuing the investigation. This contract research was ended in 1979.

Other Factors and Services Affecting Dolphin Mortality

Condition and Proper Use of Equipment

Much effort was expended on developing methods to alleviate many of the direct causes of mortality, but little had been done to address one of the more important indirect causes—malfunctions of machinery, gear, or procedures. These malfunctions were classified beginning in 1977 according to their relative contributions to dolphin mortality so that specific research areas could be identified (Table 5). Using these data, general recommendations for reducing rates and severity of some malfunctions have been prepared (Coe et al., In Press).

Operator Judgment

The captain's decisions are the most important factors influencing the outcome of tuna vessel operations. The level of experience and the amount of information he possesses help him analyze circumstances and determine the best course of action. Any application of advanced technology or refinement in fishing procedures to reduce dolphin mortality will be decided by the vessel captain. The captain must either believe in the usefulness of changes or be required to incorporate them by law. The successful transfer of technology and information is a major key to the reduction of dolphin mortality.

Of the many methods that have been employed, the most effective one is a combination of the regulatory observer program and the enforcement regime. Prior to the existence of regulations governing gear and procedures (before 1976), skipper workshops were held and informal waterfront contacts were frequent while searching for volunteer vessels and captains to carry research observers. With the establishment of the mandatory observer program and vessel operator certification requirements, skipper training sessions (with mandatory attendance) were held. The regulated gear and procedures as well as the latest developments in mortality-reduction technology were presented at these sessions. "Marketing" methods for this information were not researched.

Extension Services

In 1977, NMFS established an extension service primarily to assist captains in the proper installation and

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[13] Awbrey, F. T., T. Duffy, W. E. Evans, C. S. Johnson, W. Parks, and J. DeBeer. 1979. Summary of research results from the first leg of the third cruise of the dedicated vessel, June 22 to July 15, 1978. U.S. Dep. Commer., NOAA, NMFS, SWFC, Admin. Rep. LJ-79-11, La Jolla, Calif., 29 p.

[14] Ikehara, W. N., and J. E. Bardach. 1981. Chemosensory attracting and guiding of yellowfin tuna, *Thunnus albacares.* NOAA Contract 03-7-208-35268. U.S. Dep. Commer., NOAA, NMFS, SWFC Admin. Rep. LJ-81-07C, La Jolla, Calif., 42 p.

alignment of aprons, and also to disseminate information on other mortality-reduction techniques. The extension group monitored observer reports of incoming vessels for high kill rates and gear problems, and then met with the captains to discuss the problems on an informal basis. This work was coordinated with the NMFS Southwest Regional Office, the industry-sponsored Porpoise Rescue Foundation, and the Expert Skipper's Panel. The Expert Skipper's Panel, working directly with the extension group, has been very successful in the transfer of this information to the fleet by making captains aware of specific techniques and procedures for reducing dolphin mortality.

Discussion

The remarkable reduction of annual estimated dolphin mortality in the U.S. tuna fleet from 315,000 animals in 1970 to 16,900 animals in 1980 without any substantial changes in the basic fishing methods reflects two things. First, in 1970 there was tremendous potential for improvement in the standard tuna purse seine technology for release of dolphins without affecting fishing success. Second, the improvements were adopted by the fleet quite rapidly. The improvements, whether required by law or used voluntarily, appear to have had very little, if any, negative impact on fishing efficiency. Reductions in dolphin kill of this magnitude (from 70 animals per set in 1970 to about 3 per set in 1980) have shortened the average set duration. The improved methods and gear have been based on compatibility with existing purse seining technology, and as such have also been employed by many foreign tuna boats.

That more than a decade passed with the concentration in mortality-reduction research on the Phase-I objectives is not surprising when one considers the severity of the problem in the beginning and the fact that only one or two major field experiments aboard chartered vessels could be reasonably executed in any given fishing year. Background information and experience had to be developed before experiments could be devised, and an incredibly broad range of ideas for solutions had to be evaluated. The diversity within the fleet coupled with limited research funds made designing experiments to meet stringent statistical requirements impossible. Even when economically and logistically acceptable gear and methods were devised, their introduction into practice was slow due to the traditional nature of the evolution of fishing systems and the difficulty in communicating with operators who were at sea 200-300 days a year.

The enactment of gear and procedural regulations by NMFS, coupled with the observer program, was instrumental in helping the fleet lower its kill rates in the shortest possible time. When carrying an observer aboard his vessel, a captain was under considerable pressure to use every technique at his disposal to minimize kill, since his performance was extrapolated to the entire fleet to monitor the kill quota (beginning in 1976). The frequency of observer trips (about 1 per year per vessel) and the resulting visibility of performance has served to create a competitive atmosphere among captains, raising their motivation and competence in dolphin release to very high levels.

As long as there is a management-oriented "porpoise observer program" and the annual kill quotas are reasonably close to levels attainable by the U.S. tuna fleet using present methods, there is every reason to expect kill rates to remain relatively unchanged. Kill rates may increase over time, however, if the extension services to the fleet are not continued on a high level. Kill rates cannot be expected to decrease significantly in the absence of technological improvements, since the fleet appears to have incorporated successfully nearly all mortality-reducing measures that are presently available. Mistakes are made, however, and accidents happen; occasional high-kill sets still occur. This is to be expected since the environment, dolphin behavior, and equipment malfunctions are difficult for vessel captains to anticipate or control.

There is, however, the potential for developing fishing technology to further reduce the present dolphin kill rates. Investigations into the backdown operation had led to a basic understanding of the dynamics involved. Further investigations aimed at optimizing the configuration of the backdown channel and reducing the number and severity of canopies and premature net collapses hold a high degree of success. The idea of a dolphin-permeable backdown apex was never fully investigated and also deserves much more attention.

Information gathered on net designs from other purse seine fisheries where roll-ups do not occur would be useful in the elimination of that plaguing problem. The potential roll of model nets and computerized simulation models to investigate innovative net designs, alternative mesh configurations, and solutions to persistent mortality-related problems is great. These models also have the clear advantage of being less costly both in terms of time and money. Continued high-level support of the extension services to gather, analyze, and disseminate pertinent information on gear and machinery maintenance problems, dolphin rescue techniques, and operational procedures is very important. The timely transfer of their results and recommendations to the tuna purse seine fishery at large can be achieved through existing industry sponsored groups such as the Expert Skipper's Panel.

The results of implementing these ideas would bear directly on the kill rates of the present purse seine fleet. If reducing the total number of sets on dolphins can be considered as a partial solution to the problem, then a number of other research and development projects might be undertaken to increase the harvest efficiency for tunas not associated with dolphins.

Development of alternative fishing systems which do not entail the capture of dolphins when harvesting the associated yellowfin tuna, the full realization of the Phase-II goal, is a distant prospect. To begin addressing the idea will require a research program that is basic and broadly based, to fully delineate the nature of the tuna-dolphin bond, and to then develop a means to temporarily break or alter that bond. If these steps are satisfactorily completed, a modified fishing system to capture the tuna will then have to be devised. Such a system, of course, would have to be economically equal or superior to the present system and would have to be compatible with present-day vessel design, at least in the short run. Aside from the systematic rejection of a number of proposed solutions to this problem, very little progress has been made toward a realistic solution for the elimination of the incidental involvement of marine mammals in tuna purse seining.

Some very basic lessons have been learned in the course of this research. These lessons are generally applicable to most fishing technology problems. First, relative to industry relations:

1) In order to successfully research gear-technology problems in fisheries, the cooperation and confidence of the fishermen is essential.

2) Social systems and tradition are very important factors in the success or failure of technology transfer in fisheries.

3) Much of what fisheries technologists need to know to solve a problem is usually already known by someone in the fishery.

4) The fishing community will resist intervention regardless of how benign or progressive its intent.

Second, with regard to the conduct of applied research on fishing technology problems:

1) Enough vessel time is rarely available to adequately test and modify experimental gear and procedures.

2) In a fully operating commercial fishery, organizing and fielding a well-designed experiment is extremely difficult because a large number of variables cannot be controlled.

3) Modification of the physical performance of fishing gear is often complicated by the lack of fixed points or fulcrums from which to exert desired forces.

4) With experimental vessel time at a premium, the probability of unfavorable experimental outcomes should be minimized through extensive shoreside investigations and preparations.

5) The amount of useful information which can be derived from observations and measurements taken only at the surface is limited. Remote sensing equipment and diving capabilities are essential for complete assessment of most fishing technology problems.

6) Fishing technology tailored to accommodate the natural behavior of the animals involved has a high probability of success.

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Hawaiian monk seal diving behavior

R.L. DeLong, G.L. Kooyman, W.G. Gilmartin & T.R. Loughlin

DeLong, R.L., Kooyman, G.L., Gilmartin, W.G. & Loughlin, T.R. 1984: Hawaiian monk seal diving behavior. — Acta Zool. Fennica 172:129—131.

Diving behavior of Hawaiian monk seals was studied to gain an understanding of their use of the marine habitat. Radio tags and maximum-multiple-depth recorders (MMDR) were attached with anklets to seven adult male monk seals at Lisianski Island. 24-h automatic monitoring of radio tags provided a detailed record of hauling out activity on the island's beaches. Over 4800 individual dives by six animals were recorded by the MMDR system. The majority (59 %) of dives were in the 10—40 m depth range, the remaining dives were to depths generally greater than 40 m, with 13 dives to at least 121 m. Monk seal prey items were identified from examination of seal scat and included fish otoliths, cephalopod beaks and invertebrate exoskeleton fragments. The prey assemblage was benthic; the majority of prey were shallow water forms and a smaller number of species were deep water forms. The depth at which the prey were taken generally agreed with the distribution of monk seal dive depths recorded. This information indicated that Hawaiian monk seals depend entirely upon the food resources found over the reef surface and slopes while at rookery islands during the breeding season.

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1. Introduction

The endangered Hawaiian monk seal *Monachus schauinslandi* has breeding populations restricted to atolls of the Northwestern Hawaiian Islands. The species appears to have declined in numbers by about one-half between 1958 and 1978 and the center of abundance has shifted from the atolls in the western portion of the range to those at the eastern extreme of the breeding range (Johnson et al. 1982). Conservation efforts by the U.S. National Marine Fisheries Service include consideration of designating critical habitat under terms of the U.S. Endangered Species Act. The rookery beaches were to be included as part of critical habitat. The fact that monk seals are known to feed on benthic or reef-dwelling fishes and invertebrates argued for including marine habitat within the critical habitat, but no information existed on the depths to which monk seals commonly dive in search of prey. The need to preserve an abundant prey assemblage for monk seals was countered by an intense interest in developing commercial fisheries in the inner reef and reef slope waters. The seaward extension of the boundary of critical habitat became a major point of contention with commercial fisheries interests not wanting to be excluded from fishing any nearshore waters and resource managers recognizing that the protection of food resources within critical habitat would be essential to recovery of the endangered monk seal.

Our study was an attempt to obtain a series of dive records from feeding monk seals to provide a data base from which a seaward boundary of critical habitat could be designated. In addition we were interested in testing radio tags for determining the proportion of time animals spend ashore. This was needed to adjust census figures as an estimation method for population size.

2. Materials and methods

The study was conducted at Lisianski Island (26°02'N, 174°04'W) from 4 May through 11 June 1980. Adult male seals were selected for instrumentation because they remain on or near the rookery islands during most of the pupping season which extends from March through June. Males normally go to sea in the evening, feed during the night, and return to the island in early to mid-morning. By instrumenting only adult males we were assured that some portion of the dives would reflect the depths where animals search for food or were actually feeding. Futher, since the males are forced to return to land to obtain access to females we had a high probability of being able to recover instruments.

Seven adult males were captured by physical restraint with a canvas restraining device, a hoop net, and black bag. The canvas restraining device consisted of a heavy canvas stretcher with wooden poles which we placed over sleeping animals. Physical restraint was necessary only for instrumenting the animals and subsequent adjustment of one anklet.

Each seal was equipped with a radio transmitter on one ankle and a depth-of-dive recorder on the other. Radio transmitters were purchased from the Cedar Creek Bioelectronic Laboratory of the University of Minnesota. The transmitters were 2/5 × 8 cm cylindrical package weighing approximately 50 g in air. They transmitted on 164 MHz, were powered by a lithium battery sufficient for one to two months life, and were encapsulated in electrical casting resin. Transmitters were attached by means of an anklet of machine belting 12 mm wide and 3 mm thick, covered with 20 mm diameter latex surgical tubing. The belting was connected using a one-eighth inch brass machine bolt with brass flat washers and a steel lock washer and nut. The bimetallic combination provided certain release of the anklet should it not be recovered from the animal.

Instruments were removed with a knife blade set at the back of a stainless steel hook attached to a 1.2 m wooden handle. The ~~point of~~ the hook was slipped under the anklet and tugged sharply cutting both the surgical tubing and machine webbing, freeing the anklet.

The radio-tagged animals were monitored with a 4-element Yagi antennae and programmable scanner-receiver connected to an Esterline Angus strip-chart recorder. Two antennae were mounted on a 9-m high mast located on the highest point of the island and oriented along the long and short axis of the island.

Multiple maximum depth recorders (MMDR) were attached in the same manner as the radio transmitters. The units used were 2.3 cm in outside diameter by 9.5 cm long and weighed 95 g in air. The MMDR basically was a series of pressurse transducers and a time circuit which monitored depths of dives which were processed in eight storage registers for data readout (Kooyman et al. 1982). A potentiometer made it possible to set the span on the pressure range from 0—500 psig. The pressure ranges correspond to specific water depth ranges. Anytime a dive exceeded the threshold of a counter, the dive was added to that register's count and stored. The end result was a frequency distribution of all dives made by the seal over the period of time the MMDR was attached. The data stored in the recorder was determined by connecting the unit to a digital processor. Each register was read separately.

To assess food habits of monk seals during the study, we collected fresh scats which were soaked for 12 to 24 h in sea water to which was added ca. 1 g liquid detergent. The liquified scat were then run through a set of two nested testing sieves measuring 2.36 mm and 0.71 mm. Mard parts such as fish otoliths, bone, teeth, and scales, cephalopod beaks, and exoskeleton of lobster were removed from the sieves and stored in alcohol for later identification. Fish otoliths were identified by John E. Fitch, California Department of Fish and Game, and cephalopod beaks by Clyde Roper, U.S. Museum of Natural History, Smithsonian Institution.

Table 1. Activity of adult male Hawaiian monk seals instrumented with dive recorders and radio tags, Lisianski Island, May—June 1980.

Tag radio freq.	Dive record days	Proportion of daylight hours ashore	At sea (day/night[1])	Dives recorded	
				Number	Depth
164.192	2	0.21	0/2	108	10—40 m
164.130	7	0.20	0/5	11	10—40 m
164.113	10	0.43	0/0	7	10—40 m
164.228	20	0.30	5/13[2]	1193	10—40 m
				133	41—85 m
164.161	18	0.23	2/16[2]	1469	10—40 m
				184	41—85 m
164.099	18	0.40	1/4	Recorder damaged no record	
164.053	19	0.13	6/11[3]	75	10—30 m
				935	31—60 m
				689	61—120 m
				13	121—175 m

[1] Nights are tallied if animal was at sea from dark to midnight, midnight to dawn, or during both periods; days were tallied if animal was at sea from dawn to noon or noon to dark.

[2] Includes 2 absences of a night, day, and another night.

[3] Inclucees one absence of 4 successive days and 5 nights, and one absence of a night, day and another night.

3. Results

Dive recorders were attached for 2 to 20 days for an aggregate of 94 days. The dive recorder for one animal was inoperative. Six animals accomplished 4817 dives in 60 day or night periods at sea (Table 1) for an average of 80 dives/period at sea. The majority (59 %) of dives were in the 10—40 or 10—30 meter range, with the remaining 41 % of dives being in depths beyond the 30 to 40 meters upper threshold of the first register to depths up to at least 121 m. Only three animals were away from the island two or more nights and these were the only seals that dove to depths greater than 40 m. Due to an extensive reef system of Lisianski Island, the seals must swim 10—21 km from the island to reach water 40 m deep.

Radio tags functioned well and allowed location of instrumented males when they were ashore. The average time ashore during daylight hours for 6 reproductive adult males was 16 % during the hour following dawn, then gradually increased to 35 % between 1100—1200 hours, and decreased to 21 % in the hours preceding darkness. The proportion of time individual reproductive males were ashore varied from 13 % to 40 % of total daylight hours. A single nonreproductive adult male exhibited a pattern unlike the reproductive males. He spent 43 % of total daylight hours ashore but was ashore early morning and late evening and was frequently in the water from 1100—1600 hours. We collected all scat found on the island. We obtained identifiable hard parts from 182 of 232 scat collected. Otoliths of 260 fishes of 11 families, beaks of 71 cephalopods all of the genus *Octopus* and exoskeleton fragments of one lobster were identified. An additional 11 otoliths could not be identified from available reference material and 15 otoliths were too digested to allow identification.

4. Discussion

Lisianski Island is located on the north end of Neva Shoals — an extensive shallow water area which extends primarily south of the island. To reach the 10 meter isobath, the minimum diving depth recorded, animals needed to be from 1 to 13 km from land. Beyond Neva Shoals there are extensive coral flats within the 10—40 meter depth range where male monk seals were diving and feeding. The 40-m isobath generally delineates the outer edge of the reef. A substantial portion of the recorded dives, those beyond 30 m, reflect animals diving along the reef slope.

These are the first dive records for the Hawaiian monk seals. They suggest a pattern of generally shallow dives, yet the dives in excess of 121 m by one animal are moderately deep for pinnipeds. Several species have been recorded to dive beyond 150 m: a northern fur seal *Callorhinus ursinus* female to 190 m (Kooyman et al. 1976); a California sea lion *Zalophus californianus* male to 250 m (Ridgway 1972); a Weddell seal *Leptonychotes weddelli* to 600 m (Kooyman 1966). When compared to the dive depths accomplished by these species the 121 m (or greater) dives recorded in this study may be considerably less than the maximum diving capability of the Hawaiian monk seal.

The deep dives recorded in this study support a single diving record for the Mediterranean monk seal *Monachus monachus* which was caught on the hook of tuna gear set at a depth of 75 m at Camera de Lobos, Madeira in 1957 (Sergeant et al. 1978). There had been some question as to whether that animal might have been hooked while the gear was being set, but in light of the demonstrated diving capabilities of the Hawaiian monk seal, it is probable that the Mediterranean monk seal was caught while the gear was at depth.

Determination of the proportion of time spent ashore for adult males during daylight hours is difficult because of their tendency to lay between a female and the water's edge with their rear flippers immersed in the water. When the transmitter antenna is in wet sand or under water, the signal is attenuated and no signal is received, yet the male is almost entirely ashore. Therefore, the radio tag record underrepresents the actual proportion of time ashore.

Results of the scat collection indicate that the Hawaiian monk seal feeds heavily on reef fishes. The fish found most frequently and in highest numbers were conger eels (Congridae), surgeon fish (Acanthuridae), and wrasses (Labridae) which prefer shallow, benthic habitats. Less numerous were brotulids (Brotulidae) and cusk eels (Ophididae) which are probably found in both shallow and deep, benthic habitats, and lizard fish (Synodidae) were the only prey species from a deep water, benthic habitat. The habitat depth of the identified prey is consistent with distribution of the monk seal dive depth records. During the breeding season monk seals apparently depend entirely on the food resources found on the coral reefs, sandy flats, and deeper reef slopes. A designation of critical habitat which included all waters from island shorelines to the reef slope edge is justified by the marine habitat utilization data obtained in our study. Setting the seaward boundary of critical habitat at 20 fathoms would include most of those waters and provide a consistent boundary which could be easily detected by vessel operators approaching the rookery islands of the Hawaiian monk seal.

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Review of Techniques Used to Estimate the Average Age at Attainment of Sexual Maturity in Marine Mammals

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ABSTRACT

The average age of sexual maturation (ASM) is generally used as a 'K' index to determine whether or not a population is approaching its carrying capacity. If the ASM is increasing, it is inferred that the density *per capita* of resources is increasing and that density-dependent mechanisms are operative. At least five techniques are commonly used to estimate the ASM. These techniques are mean of known-age first-time ovulators, mean deduced from age-specific ovulation rates, regression of age-specific ovulation rates versus age, graphical interpretation of age when 50% of animals have ovulated, and graphical interpretation of age at which the cumulative probability of ovulation equals the cumulative probability of not ovulating. Using hypothetical data, it is shown that different techniques produce different estimates of the ASM. The mean of known-age first-time ovulators is assumed to be the best estimator of the ASM, and other techniques are compared for bias and precision.

INTRODUCTION

The average age at attainment of sexual maturity (ASM) refers to the average age at which females in a population ovulate for the first time. This life history parameter has been used to compare the status of marine mammal populations by assuming that a population which has a higher density will have a greater average ASM. It has been used in population models (see Eberhardt and Siniff, 1977, and Goodman, 1984) that require an estimate of the average age of first birth, which is estimated by adding the average ASM and the average duration of the first gestation period.

The average ASM can be and has been estimated in a number of different ways and from a number of different data sources. Five different estimators are in common use. They are mean age of first-time ovulators (e.g. Bengtson and Siniff, 1981), mean deduced from age-specific ovulation rates (DeMaster, 1978), regression of corpora counts versus age (e.g. Kasuya, 1972), graphical interpretation of a plot of percentage mature against age to determine the age when 50% of females have ovulated at least once (e.g. Perrin, Holts and Miller, 1977), and graphical interpretation of age at which the cumulative probability of ovulating by age x equals the cumulative probability of not ovulating at age x or older (Kasuya, 1972). The purpose of this paper is to compare the estimates of ASM values for each of the five estimators with the same hypothetical data set and to compare the variance of the estimators that utilize age-specific rates of ovulation. It is my intention to show that each estimator will produce a different estimate of the average ASM, and that comparisons made between different populations or the same population over time must be based on estimates of the ASM that are derived in the same manner. This can be a particular problem when comparing the results of one study with published results of another where the method used to estimate the average ASM may not be given.

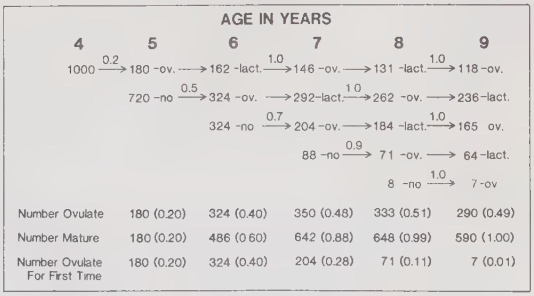
METHODS

Comparison of ASM estimators

A hypothetical data set of age-specific ovulation rates was derived by assuming the following: annual survivorship of females is constant and equal to 0.90; no animals less than 4 years of age ovulate; 20% of 4-year-olds ovulate; 50% of 5-year-olds that did not ovulate as 4-year-olds ovulate; 70% of all 6-year-olds that did not ovulate as 5-year-olds ovulate; 90% of all 7-year-olds that did not ovulate as 6-year-olds ovulate; and all 8-year-olds that did not ovulate as 7-year-olds ovulate. It was further assumed that animals that ovulated at age x will not ovulate again until age $x+2$, but at these ages all animals will ovulate independent of age. This simulates a reproductive interval of 2 years. The number of animals that ovulate for the first time at age x and the total number of ovulating animals at age x, under these assumptions, are presented in Fig. 1. The age-specific ovulation rates and number of first-time ovulators were used to estimate the average ASM for each of the five techniques.

Sensitivity analysis

A sensitivity analysis was performed on the three ASM estimators that utilize age-specific ovulation rates: the mean deduced from age-specific ovulation rates, the age


AGE IN YEARS
4
5
6
7
8
9
1000 —0.2→ 180 -ov. → 162 -lact. —1.0→ 146 -ov. → 131 -lact. —1.0→ 118 -ov.
720 -no —0.5→ 324 -ov. → 292-lact. —1.0→ 262 -ov. → 236-lact.
324 -no —0.7→ 204 -ov. → 184 -lact. —1.0→ 165 ov.
88 -no —0.9→ 71 -ov. → 64 -lact.
8 -no —1.0→ 7 -ov

	5	6	7	8	9
Number Ovulate	180 (0.20)	324 (0.40)	350 (0.48)	333 (0.51)	290 (0.49)
Number Mature	180 (0.20)	486 (0.60)	642 (0.88)	648 (0.99)	590 (1.00)
Number Ovulate For First Time	180 (0.20)	324 (0.40)	204 (0.28)	71 (0.11)	7 (0.01)

Fig. 1. Summary of hypothetical population of female dolphins. Annual survivorship equals 0.90, and the reproductive interval is 2 years.

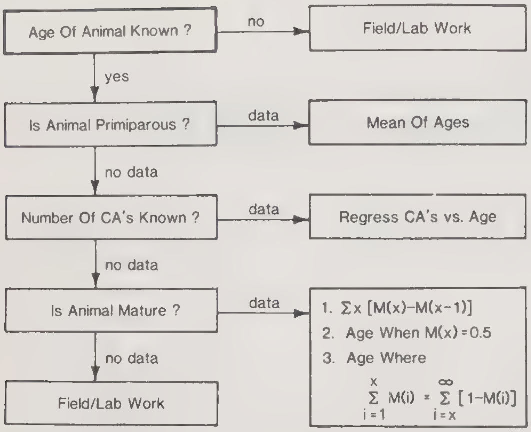


Fig. 2. Summary of which estimators for ASM are used with certain data bases.

where 50% of females are mature (i.e. they have ovulated at least once), and the age where the cumulative probability of previous ovulation equals the cumulative probability of not having ovulated. A series of age-specific ovulation rates were selected at random from a normal distribution, with means equal to the rates given in Fig. 1, and a coefficient of variance equal to 0.025. For each of the 3 estimators, 30 sets of age-specific ovulation rates were generated and estimates of the average ASM derived. This type of Monte Carlo simulation represents a situation where only the sampling variation is being compared. The biological parameters are assumed to remain constant between samples.

Additional consideration

Problems with obtaining precise, unbiased estimates of age were not considered in this review. It was assumed that animals that have been collected can be aged correctly. Problems in identifying corpora and questions of corpora regression and persistence were not addressed. It was assumed that all of the different estimators suffer from these problems, but future efforts should be directed at determining whether all of the estimators are equally sensitive to them. It was also assumed that the mean age of first-time ovulators is an unbiased estimate of the average of ASM. However, sample sizes of ovaries from animals that have ovulated only once are generally small, and estimates based on all ovaries sampled are more common. If counts of total corpora albicantia (CAs) in both ovaries are available, it is possible to regress number of CAs against age. However, if only information on presence or absence of CAs is collected, then one of the three alternative estimators must be used (Fig. 2 summarizes the various analyses and data requirements). Finally, some authors have estimated the length where 50% of all females were sexually mature, and then estimated the ASM from a derived relationship between length and age (e.g. Perrin *et al.*, 1977). This estimator was not considered, as it could not be determined from the data given in Fig. 1.

RESULTS

Comparison of estimators

1. *Mean age of first-time ovulators*

The mean age of first-time ovulators (AFO) is generally accepted as an unbiased estimate of the ASM. However, the sample size for this estimator is often very small, making it relatively imprecise. The mean AFO from the hypothetical population (Fig. 1) is 6.24 years (Table 1). Two advantages of this technique over the other estimators are that it is unbiased and that confidence intervals are easily constructed from the standard formula for the variance of a mean.

2. *Mean deduced from age-specific ovulation rates*

The derivation of this estimator and its variance is given in DeMaster (1978). The mean deduced from age-specific ovulation rates (ASOR) is a positively biased estimator. This is because the estimator evenly weights all of the age classes, when older age classes clearly comprise less of the population than do younger age classes (see Table 1 for formula). Therefore, this bias is progressively worse as the annual mortality rate increases. For an annual mortality rate of 0.10, the mean of ASOR is 6.33 years (Table 1; Fig. 3). If the age structure is known, an unbiased estimate of the ASM can be made with this estimator:

$$\text{ASM} = \sum_{x=0}^{\infty} \left[[M(x)-M(x-1)](x)f(x) \middle/ \sum_{x=0}^{\infty} (fx) \right]$$

where $M(x)$ equals the proportion of x-year-old females that are mature, x is the age, and $f(x)$ is the number of animals x years old.

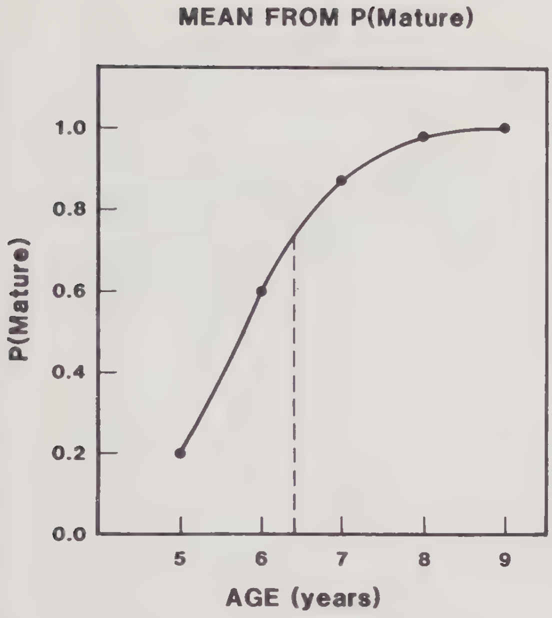
3. *Age where proportion mature equals* 0.50

The age where 50% of the animals are mature (50% age) is a commonly used estimate of the ASM (Perrin *et al.*, 1977; Kasuya, 1976). The estimate is usually made by interpreting a plot of percent mature versus age (see Fig. 4).

Table 1

Summary of five ASM estimators. All estimates of ASM were made with the same data set (Fig. 1). $M(x)$ is the proportion of x-year-old females that were mature, and x is the age in years. In methods 1 and 2, the summation is over all ages

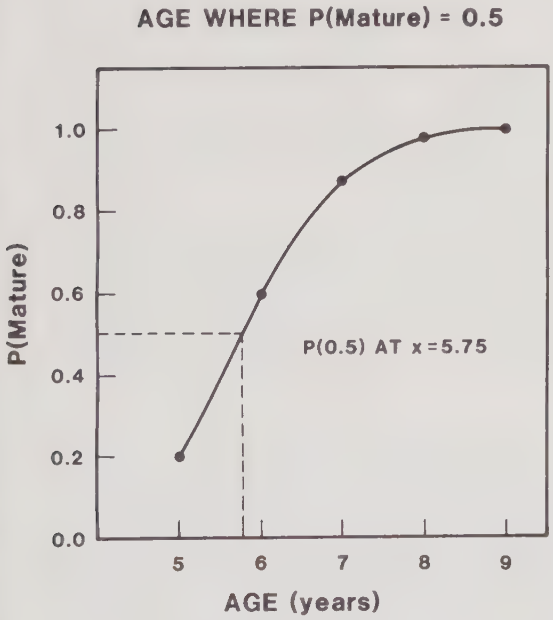
1. Mean of ages:	$\frac{\Sigma(\#\text{ ovulate for the first time})\times}{\text{total number in sample}}$	= 6.24 years
2. Mean from P(mature):	$\Sigma[M(x)-M(x-1)]x$	= 6.33 years
3. Age where P(mature) = 0.5:		= 5.75 years
4. Age where	$\sum_{i=1}^{x} M(i) = \sum_{i=x}^{\infty}[1-M(i)]$:	= 5.81 years
5. Regression of # CAs vs age; age where # CAs = 1.0		= 6.77 years



$$ASM=\sum x\,[M(x)-M(x-1)]=6.33$$

$$=(5)(0.2)+(6)(0.4)+7(0.28)+8(0.11)+9(0.01)$$

Fig. 3. Plot of age versus percent mature (ASOR).



$$\frac{0.5-0.6}{0.2-0.6}=\frac{x-6}{5-6}$$

$$x=5.75$$

Fig. 4. Plot of age versus percent mature (50%).

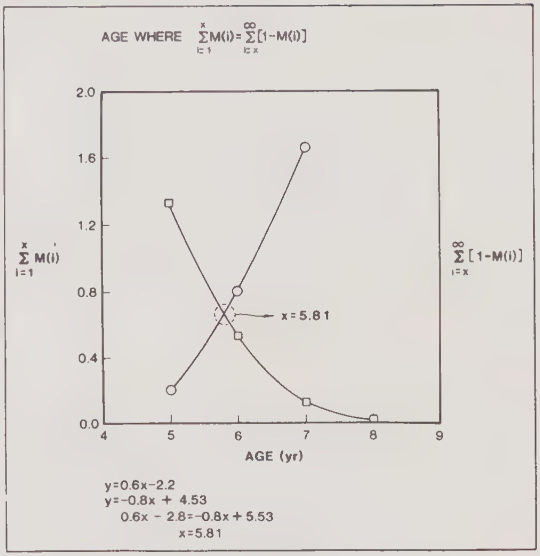


Fig. 5. Plot of terms used to estimate ASM with summation technique.

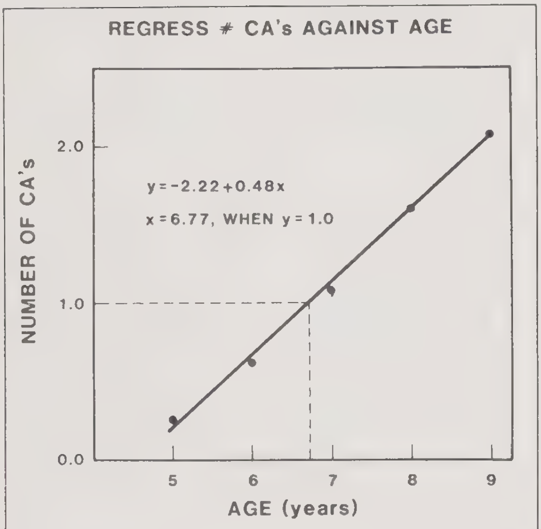
A standardized procedure for modeling the age-versus-percent-mature relationship has not been devised. If the shape of this relationship is symmetric with age, the age where 50% of animals are mature will be similar to the mean of the proportion mature. However, in general this relationship rapidly increases during the early ages and then only slowly increases to unity for the latter ages. In this case the mean AFO will generally be greater than the 50% age. In the hypothetical data set, the 50% age was approximately 5.75 years (Table 1). Variance estimates have not been developed for this estimator of ASM.

4. *Summation estimate*

The fourth ASM estimator (referred to hereafter as the summation procedure) was first described by Kasuya (1972) and subsequently used by Kasuya *et al.* (1974). The summation procedure estimates the ASM as the age where the summation of the proportion mature from birth to the ASM equals the summation of one minus the proportion mature from the ASM to the maximum age (see Table 1 for formula). Kasuya (1972) recommends this procedure over the 50% age method when sample sizes for individual age classes are small. The estimated ASM using the summation procedure and data from Fig. 1 is 5.81 years (Fig. 5). A derivation of this estimator's variance has not been developed, and, therefore, confidence intervals are generally not given. It must also be assumed in using the estimate (and the previous estimate) that a straight line adequately describes the relationship around the ASM.

5. *Regression of the number of CAs versus age*

The final estimator (referred to as the regression estimate) regresses the number of corpora albicantia against age (Fig. 6). The ASM is derived from the regression equation by estimating the age where the number of CAs is greater than zero. In using this technique it is necessary to assume that all ovulations are 'recorded' in the ovaries as



	# CA's				
	0	1	2	3	MEAN
AGE 5	80	20	-	-	0.2
6	40	60	-	-	0.6
7	12	68	20	-	1.08
8	1	39	60	-	1.59
9	-	12	68	20	2.08

Fig. 6. Plot of number of CAs versus age.

permanent scars and that the ovulation rate is constant with age. The technique has a disadvantage in that it is positively biased whenever the reproductive interval is greater than 1 year. This is because animals with reproductive intervals greater than 1.0 often have the same number of CAs in consecutive years. This tends to make the age where the average number of CAs is equal to 1.0 greater than the average age of first-time ovulation. Also, variation in attaining maturity must be taken into account when fitting an ovulation-rate curve (see Perrin and Reilly, 1984). Using the data in Fig. 1, the regression estimate of the ASM is 6.77 years (Table 1). Confidence intervals can be derived with standard procedures for estimating the variance around the regression line, but this will provide an underestimate of the variance of the ASM.

Sensitivity Analysis

The results of the sensitivity analysis indicate the three techniques are equally precise (Table 2). In other words, one estimate does not have a relatively smaller confidence interval than another. Perhaps different results would be obtained with a simulation if the coefficient of variation were larger. This should be explored in the future.

Table 2

Summary of three different ASM estimators, where identical data set was used to calculate the means, confidence interval, and coefficient of variance

ASM estimator	$\bar{x} \pm 2$ S.E.	C.V.
ASOR	6.34±0.196	0.0079
50% age	5.75±0.164	0.0071
Summation	5.81±0.180	0.0079

DISCUSSION

The ASM of a population is currently used to compare the 'status' of different populations. This assumes that the ASM is dependent on density *per capita* of resources. When used in this manner, there is a clear advantage in using those estimates that have accompanying variance estimates (AFO, ASOR, and the regression estimate). However, in those cases where the ASM is used as a discrete parameter in a population model, this advantage is no longer paramount. In such cases, one needs to consider the relative bias of each estimator. For two of the estimators, the direction of the bias will be known. That is, estimates based on ASOR and regression will usually be positively biased relative to the AFO estimator. The bias of the two graphical techniques is not consistent but depends on the form of the relationship between age and percent mature. In general, these estimators will underestimate the true mean. In making management-oriented decisions it may be necessary to consider what the expected bias is. In most cases, an overestimate of the true mean will result in a lower estimate of the replacement yield.

CONCLUSION

The point of this paper is not to encourage the sole use of any one technique in estimating the mean age at attainment of sexual maturity. In making statistical comparisons between populations, one seems to be limited to one of three estimators for which variances can be easily derived.

Authors should be encouraged to be consistent in their usage of ASM statistics. I recommend that the following guidelines be followed:

(1) age-specific ovulation rates should be given,
(2) the procedure used to calculate the ASM should be stated explicitly, and
(3) ASMs from different population should not be compared unless the same/estimation technique was used, or comparison should be suitably qualified.

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BIOCHEMICAL IDENTIFICATION OF A BLUEFIN TUNA ESTABLISHES A NEW CALIFORNIA SIZE RECORD

Large tunas are not commonly taken off the California coast and although stories exist of sightings of large yellowfin, *Thunnus albacares,* bluefin, *T. thynnus,* and bigeye, *T. obesus,* tunas, the current California size records for these species are 204 kg, 203 kg and 197 kg, respectively (Miller and Lea 1976). On 7 December 1981 a large tuna was captured in a shark gill net that was set 19.3 km south of Anacapa Island (lat 33°48.5′N, long 119°20.6′W). The fish was frozen after capture and sold 7 days later before a positive identification could be made. At the time of sale the fish's weight was determined in the round on a calibrated electronic scale to be 237 kg.

Few measurements were made of the tuna before it was butchered and sold. The total length was determined with a ruler to be approximately 198 cm. No photographs were taken of the fish, but the following physical description was offered by Mr. David Ptak, general manager of Chesapeake Fish Company: the fish was dark blue or black above and grayish white below, with some lighter vertical bars on the sides; the pectoral fins were short to moderate, reaching the 10th or 11th dorsal spine; the finlets were yellow; and the liver had a large central lobe with two lesser lobes, all of which were heavily striated on the ventral surface.

This description indicated that the large tuna, which would be a size record for any *Thunnus* species in California, was either a bluefin or bigeye tuna. Yellowfin tuna do not have striations of the ventral liver surface, whereas both bluefin and bigeye tuna may have completely striated ventral liver surfaces (Gibbs and Collette 1967). Bluefin and bigeye tuna can be separated on the basis of gillraker counts; however, gillraker counts were not made on the specimen and the head of the fish was not saved.

Due to a lack of meristic and morphometric data for the specimen, an alternate method of identification was employed. The relationships of scombrid fishes have been investigated with electrophoretic techniques and all *Thunnus* species can be distinguished on the basis of fixed allelic differences at one or more loci (Sharp and Pirages 1978). Bluefin and bigeye tuna can be separated by a fixed allelic difference at the glyceraldehyde-3-phosphate dehydrogenase (G-3-PDH) locus, an enzyme which occurs in high concentrations in tuna white muscle (Sharp and Pirages 1978). Fortunately, a small amount of the tuna's muscle had been maintained frozen by Mr. Ptak and was generously made available to the authors for an electrophoretic determination of its specific identity.

Samples of the tuna's muscle were run with samples of bigeye tuna and albacore, *T. alalunga,* muscle (frozen bluefin tuna muscle was not available for comparative purposes). Sample preparation and electrophoretic protocol followed the procedures of Graves and Rosenblatt (1980). A photograph of a gel slice stained for G-3-PDH activity is presented in Figure 1. The large tuna possessed an allele which had considerably slower anodal mobility than that of the bigeye tuna, yet slightly faster than that of the albacore. The mobility of the allele of the large tuna relative to the bigeye and albacore was similar to that reported for bluefin tuna by Sharp and Pirages (1978).

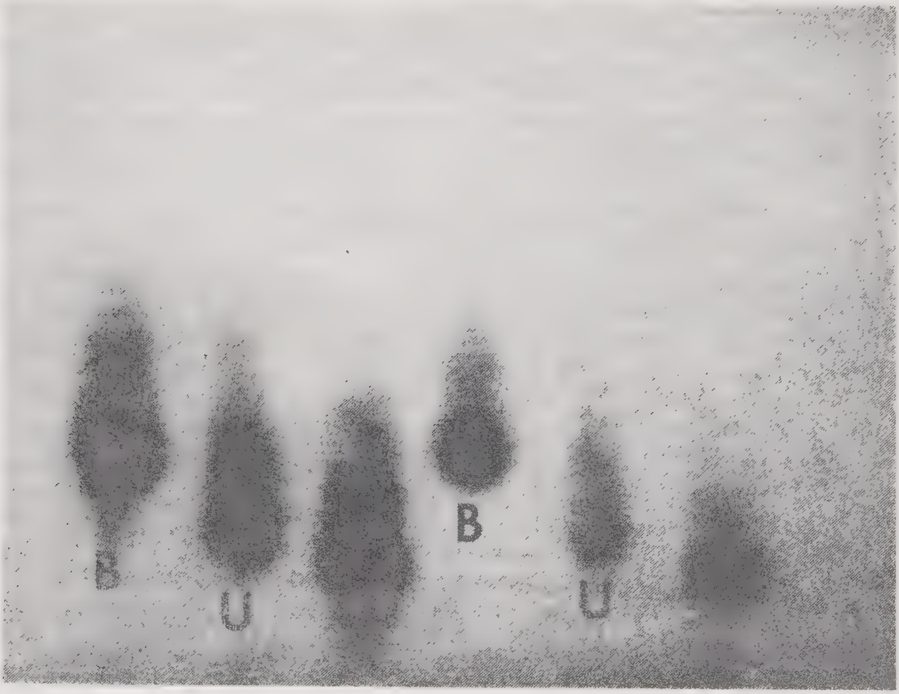

FIGURE 1. Electrophoretic mobilities of G-3-PDH alleles from three *Thunnus* species. Different stain intensities are the result of different tissue to grinding buffer ratios. B = bigeye tuna, U = unknown tuna (bluefin) and A = albacore tuna.

Although direct comparison with bluefin G-3-PDH was not possible, the large fish can be identified with confidence. The presence of striations on the liver of the specimen showed that it was not a yellowfin tuna. Because bigeye and bluefin tunas of the eastern Pacific are fixed for different alleles at the G-3-PDH locus, the lack of identity of the large tuna allele with that of the bigeye tuna demonstrated that the large tuna was not a bigeye tuna, and consequently must have been a bluefin. Furthermore, the mobility of the large tuna's G-3-PDH allele relative to that of the bigeye tuna and albacore was similar to that reported for bluefin tuna run under similar electrophoretic conditions (Sharp and Pirages 1978). On the basis of these results we conclude that the 237 kg tuna caught off Anacapa Island on 7 December 1981 was a bluefin tuna. This catch marks a substantial increase in the maximum size reported for this species in California waters.

Addendum: Since the paper has been edited a 180 kg bluefin tuna was speared off Guadalupe Island, Mexico during September 1982 and postively identified on the basis of morphological characters. In a direct electrophoretic comparison of muscle G-3-PDH, the mobilities of this bluefin and the 237 kg specimen were identical, providing positive evidence that the 237 kg fish was in fact a bluefin tuna.

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CONVERSIONS BETWEEN TOTAL, FORK, AND STANDARD LENGTHS IN 35 SPECIES OF *SEBASTES* FROM CALIFORNIA

In recent years, the rockfishes (Scorpaenidae: *Sebastes*) of the northeastern Pacific Ocean have been investigated extensively. With many institutions studying diverse aspects of their biology and fisheries, a lack of standardized methods has hampered attempts to synthesize the data. A particular problem has been the reporting of different length measurements. To provide the means to convert one of these length measurements to another, we report here the linear regression statistics necessary for conversions in 35 species of *Sebastes*.

Specimens were collected from fishery catches between Cape Blanco, Oreg., and San Diego, Calif., during 1977-82. The sample included five fish for each centimeter of body length throughout the size range of each species. Measurements were taken on a meter board in millimeters on frozen, then thawed, carcasses. Standard length was measured from the anterior tip of the upper jaw to the posterior end of the vertebral column (Hubbs and Lagler 1970:25); fork length was measured from the anterior tip of the longest jaw to the median point of the caudal fin; and the total length was measured from the most anterior tip of the longest jaw to the most posterior part of the tail when the caudal rays are squeezed together (Holt 1959:71). Linear regressions were run on all combinations of the measurements of length. Outliers (±3.0 standard deviations) from the line were noted by the computer program, then checked for data entry error and corrected when possible. If a data entry error was not found, an outlier was assumed to result from measurement error and the observation was deleted.

Statistics reported for each species are y-intercept (α), slope (β), standard error of estimate ($S_{y \cdot x}$), correlation coefficient (r), range in length, and the sample size used in the regression (n) (Tables 1-3). Estimates of α imply impossible values for the dependent variable when the independent variable is zero. The impossible results could be caused by random error in estimation of α or nonlinearity for values less than those observed. The high values of r and examination of scattergrams indicate that the length relationships are linear over the observed range of values. The standard precaution of limiting the application of these regressions to the ranges of observed values is advised. To calculate the total length (TL) of *S. alutus*, given a standard length (SL) of 250 mm, the regression values from Table 1, total length on standard length, are used so that

TABLE 1.—Results of linear regressions of standard length versus total length for *Sebastes*. Measurements are in millimeters.

Species of *Sebastes*			Standard length		Total length on standard length			Standard length on total length		
	n	*r*	Min	Max	α	β	$S_{y.x}$	α	β	$S_{y.x}$
alutus	49	0.995	232	361	1.454	1.249	3.746	2.056	0.792	2.984
auriculatus	116	1.000	72	426	−1.423	1.240	3.787	1.369	0.806	3.054
aurora	43	0.991	164	324	0.098	1.220	4.709	4.398	0.806	3.827
babcocki	74	0.999	185	532	6.478	1.196	4.833	−4.614	0.834	4.035
carnatus	105	0.999	75	292	3.676	1.201	2.206	−2.866	0.832	1.836
caurinus	113	0.997	111	443	3.873	1.209	5.769	−0.653	0.820	4.568
chlorostictus	107	0.999	107	382	5.316	1.202	3.636	−3.931	0.830	3.023
chrysomelas	60	0.998	77	316	1.007	1.211	3.161	−0.123	0.822	2.605
constellatus	105	0.999	148	365	4.497	1.175	3.119	−3.204	0.849	2.651
crameri	102	0.999	102	394	−0.304	1.266	4.153	0.737	0.788	3.278
diploproa	80	0.999	87	308	1.286	1.242	2.718	−0.740	0.804	2.188
elongatus	108	0.998	107	317	15.238	1.165	3.543	−12.144	0.855	3.036
entomelas	105	0.998	194	435	9.496	1.211	5.679	−6.296	0.822	4.679
flavidus	193	0.997	191	453	0.468	1.247	5.700	1.379	0.798	4.558
goodei	99	1.000	101	449	4.199	1.224	2.870	−3.196	0.816	2.344
hopkinsi	71	0.993	99	251	3.059	1.200	4.788	−0.195	0.822	3.964
jordani	145	0.998	77	260	4.610	1.216	2.903	−3.128	0.819	2.382
levis	31	1.000	190	717	−4.500	1.248	4.907	3.813	0.801	3.932
maliger	42	0.996	174	397	1.463	1.220	5.639	1.120	0.813	4.604
melanops	138	0.999	74	495	7.724	1.221	5.193	−5.596	0.817	4.247
melanostomus	87	0.994	207	421	−0.954	1.244	6.897	4.780	0.794	5.508
miniatus	109	0.994	237	550	9.629	1.229	9.765	−3.095	0.804	7.900
mystinus	163	0.998	102	387	2.930	1.238	5.694	−1.192	0.804	4.588
nebulosus	69	0.995	213	366	4.294	1.196	3.962	−0.731	0.828	3.296
ovalis	83	0.997	181	375	0.550	1.225	4.374	1.329	0.811	3.558
paucispinis	163	0.999	103	649	−5.035	1.262	7.550	4.882	0.790	5.974
pinniger	136	0.997	196	565	11.476	1.239	8.002	−7.447	0.803	6.443
rosaceus	83	0.996	132	263	3.917	1.199	2.867	−1.794	0.828	2.383
rosenblatti	104	0.999	132	428	9.567	1.182	3.653	−7.374	0.844	3.086
ruberrimus	118	0.996	203	565	5.856	1.202	9.465	−1.717	0.826	7.843
rufus	26	0.999	152	447	12.946	1.177	5.963	−10.316	0.848	5.061
saxicola	68	0.999	109	288	3.226	1.242	2.456	−2.252	0.804	1.976
semicinctus	31	0.979	101	147	8.179	1.170	3.617	−1.752	0.820	3.027
serranoides	129	0.995	190	441	8.292	1.209	7.277	−3.542	0.819	5.988
wilsoni	48	0.999	71	126	0.572	1.234	1.071	−0.231	0.808	0.868

TABLE 2.—Results of linear regressions of standard length versus fork length for *Sebastes*. Measurements are in millimeters.

Species of *Sebastes*			Standard length		Fork length on standard length			Standard length on fork length		
	n	*r*	Min	Max	α	β	$S_{y.x}$	α	β	$S_{y.x}$
alutus	48	0.996	232	361	−0.281	1.195	3.024	2.492	0.831	2.521
auriculatus	114	0.999	72	426	−0.369	1.228	4.126	0.575	0.813	3.358
aurora	44	0.993	164	324	−3.046	1.201	4.237	6.237	0.821	3.502
babcocki	76	0.999	185	532	9.034	1.153	5.190	−6.860	0.865	4.496
carnatus	104	0.999	75	292	4.601	1.194	2.425	−3.613	0.836	2.030
caurinus	117	0.996	111	448	5.896	1.187	6.764	−2.272	0.836	5.674
chlorostictus	107	0.999	107	382	5.289	1.171	3.719	−3.987	0.852	3.173
chrysomelas	58	0.997	77	226	1.137	1.209	3.209	−0.009	0.822	2.647
constellatus	107	0.999	148	365	3.883	1.152	2.964	−2.774	0.866	2.571
crameri	103	0.999	102	394	1.390	1.205	4.282	−0.565	0.828	3.550
diploproa	82	0.999	87	308	2.092	1.181	2.627	−1.460	0.845	2.223
elongatus	116	0.998	107	317	14.186	1.116	3.469	−11.724	0.892	3.102
entomelas	106	0.997	194	435	16.964	1.124	5.602	−13.326	0.885	4.970
flavidus	198	0.998	191	453	−0.918	1.213	5.367	2.363	0.820	4.412
goodei	99	1.000	101	449	1.515	1.159	3.085	−0.988	0.862	2.660
hopkinsi	72	0.994	99	251	3.011	1.153	4.465	−0.372	0.856	3.847
jordani	154	0.998	77	260	5.645	1.124	2.519	−4.418	0.887	2.238
levis	34	0.999	190	717	0.033	1.177	8.446	0.688	0.848	7.169
maliger	41	0.997	174	397	11.835	1.173	4.867	−8.202	0.848	4.138
melanops	135	0.999	74	495	7.149	1.197	5.042	−5.247	0.834	4.209
melanostomus	86	0.994	207	421	−0.828	1.201	6.853	4.912	0.822	5.670
miniatus	106	0.994	237	550	16.442	1.168	9.200	−9.445	0.847	7.836
mystinus	164	0.998	102	387	0.352	1.192	4.975	0.644	0.836	4.166
nebulosus	71	0.993	213	366	6.934	1.181	4.623	−1.852	0.835	3.888
ovalis	83	0.996	181	375	−3.554	1.187	4.677	5.130	0.836	3.925
paucispinis	162	0.999	103	649	−4.082	1.209	6.819	4.183	0.826	5.636
pinniger	138	0.998	196	565	12.880	1.164	7.440	−9.326	0.855	6.378
rosaceus	83	0.997	132	263	1.399	1.187	2.730	0.225	0.837	2.293
rosenblatti	104	0.999	132	428	9.938	1.147	3.347	−8.023	0.870	2.915
ruberrimus	118	0.996	203	565	6.665	1.181	9.028	−2.664	0.841	7.620

TABLE 2.— *Continued*

Species of *Sebastes*	n	r	Standard length Min	Standard length Max	Fork length on standard length α	β	$S_{Y \cdot X}$	Standard length on fork length α	β	$S_{Y \cdot X}$
rufus	26	0.999	152	447	14.246	1.112	4.416	−12.392	0.898	3.969
saxicola	77	0.999	109	288	3.234	1.200	2.511	−2.315	0.831	2.090
semicinctus	31	0.978	101	147	6.486	1.128	3.562	−0.343	0.849	3.091
serranoides	126	0.995	190	441	4.422	1.184	6.779	−0.672	0.837	5.700
wilsoni	53	0.999	71	126	0.671	1.203	0.884	−0.372	0.830	0.734

TABLE 3.—Results of linear regressions of fork length versus total length for *Sebastes*. Measurements are in millimeters.

Species of *Sebastes*	n	r	Fork length Min	Fork length Max	Total length on fork length α	β	$S_{Y \cdot X}$	Fork length on total length α	β	$S_{Y \cdot X}$
alutus	48	0.999	278	430	−0.003	1.050	1.483	1.321	0.949	1.272
auriculatus	113	1.000	90	529	−0.586	1.007	1.637	0.634	0.993	1.626
aurora	43	0.998	198	388	2.293	1.019	2.349	−0.917	0.977	2.300
babcocki	72	1.000	222	635	−1.146	1.032	2.392	1.336	0.968	2.316
carnatus	101	1.000	92	351	−0.759	1.005	0.510	0.768	0.995	0.507
caurinus	107	0.999	135	538	0.629	1.010	3.022	0.005	0.988	2.988
chlorostictus	106	1.000	127	449	−0.723	1.028	1.905	0.858	0.972	1.852
chrysomelas[1]										
constellatus	104	1.000	174	422	−0.134	1.023	1.504	0.301	0.977	1.470
crameri	99	1.000	124	480	−1.700	1.051	2.002	1.756	0.951	1.904
diploproa	80	1.000	106	364	−0.558	1.049	1.704	0.669	0.953	1.625
elongatus	102	1.000	129	360	−0.552	1.047	1.449	0.701	0.954	1.383
entomelas	100	0.999	231	496	−6.845	1.072	3.251	6.954	0.931	3.029
flavidus	191	1.000	226	551	2.358	1.025	2.439	−1.906	0.974	2.377
goodei	96	1.000	122	527	2.468	1.057	2.647	−2.096	0.945	2.503
hopkinsi	70	0.999	115	292	0.002	1.041	1.917	0.428	0.959	1.840
jordani	140	0.999	89	296	−1.872	1.086	1.885	2.036	0.920	1.735
levis	34	1.000	228	855	−3.335	1.055	4.452	3.369	0.947	4.219
maliger	40	0.999	215	480	−8.696	1.034	2.782	9.075	0.965	2.687
melanops	132	1.000	91	599	1.595	1.017	2.099	−1.421	0.983	2.063
melanostomus	82	0.999	247	519	−0.635	1.036	2.181	1.065	0.964	2.103
miniatus	103	0.999	293	654	−7.857	1.054	4.638	8.665	0.946	4.394
mystinus	158	1.000	122	463	2.495	1.039	2.329	−2.164	0.962	2.241
nebulosus	71	1.000	256	498	0.854	1.001	1.423	−0.487	0.998	1.420
ovalis	78	0.999	225	438	3.914	1.033	1.996	−3.311	0.967	1.931
paucispinis	157	1.000	123	781	−0.870	1.045	2.273	0.930	0.956	2.174
pinniger	132	1.000	235	586	−4.107	1.070	2.822	4.108	0.934	2.638
rosaceus	79	0.999	158	316	1.409	1.015	1.173	−1.085	0.984	1.155
rosenblatti	103	1.000	155	497	−0.453	1.030	2.026	0.692	0.970	1.966
ruberrimus	118	1.000	243	680	−0.758	1.018	3.640	1.296	0.981	3.573
rufus	24	1.000	182	517	−2.197	1.057	1.659	2.135	0.946	1.569
saxicola	69	0.999	136	347	−0.669	1.038	2.009	0.921	0.963	1.935
semicinctus	29	0.998	119	174	−0.422	1.050	1.178	1.010	0.949	1.120
serranoides	125	0.999	222	518	1.419	1.029	2.623	−0.862	0.971	2.548
wilsoni	45	1.000	86	151	−1.141	1.035	0.560	1.182	0.966	0.541

[1] No regression was run because total length and fork length are equal.

$$
\begin{aligned}
\mathrm{TL} &= \alpha + \beta\,(\mathrm{SL}) \\
\mathrm{TL} &= 1.454 + (1.249)\,(250) \\
\mathrm{TL} &= 313.7 \text{ mm.}
\end{aligned}
$$

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SPAWNING AND GONADAL MATURATION OF THE EHU, *ETELIS CARBUNCULUS*, IN THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

Ehu, *Etelis carbunculus*, ovaries were collected from various banks throughout the Northwestern Hawaiian Islands during 1977-81. Ovaries were microscopically examined to determine the most advanced developmental stage. Mean monthly gonadal somatic indices indicated that maturation began in May and spawning occurred from July to September. Ehu were found to be serial spawners, i.e., they spawned multiple batches of ova during the season. Most females spawned by the time they reached 35 to 40-cm fork length and older (>45 cm) fish were found to remain in spawning condition longer. The overall sex ratio in a pooled sample of 833 ehu was in favor of females by 2:1. Females also predominated in the larger size ranges (45 to 65-cm fork length) and during certain times of the year, indicating possibly that they live longer or aggregate during spawning. Fecundity of ehu 38.3 to 50.8 cm was estimated at 349,500 to 1,325,600 ova.

ehu
ova
sex ratio
maturation
spawning
fecundity

INTRODUCTION

In 1976, following the enactment of the Magnuson Fishery Conservation and Management Act (FCMA), the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service (NMFS), in cooperation with the U.S. Fish and Wildlife Service (FWS) and the Division of Aquatic Resources (DAR), Hawaii Department of Land and Natural Resources (DLNR), initiated a 5-year assessment of the marine and terrestrial resources in the

Northwestern Hawaiian Islands (NWHI). An important goal of this study was to describe the distribution and abundance of commercially valuable deepwater snapper. Ehu or red snapper, Etelis carbunculus Cuvier, was the bottomfish species most frequently caught (in numbers) during this period. It ranked third in total weight. Little is known about reproduction in Hawaiian deepwater snappers and there has been nothing reported on the spawning and maturation of ehu. To better understand the recruitment of this species into the fishery, a study was initiated to determine the ehu's spawning season, fecundity, and other important aspects of its reproductive potential.

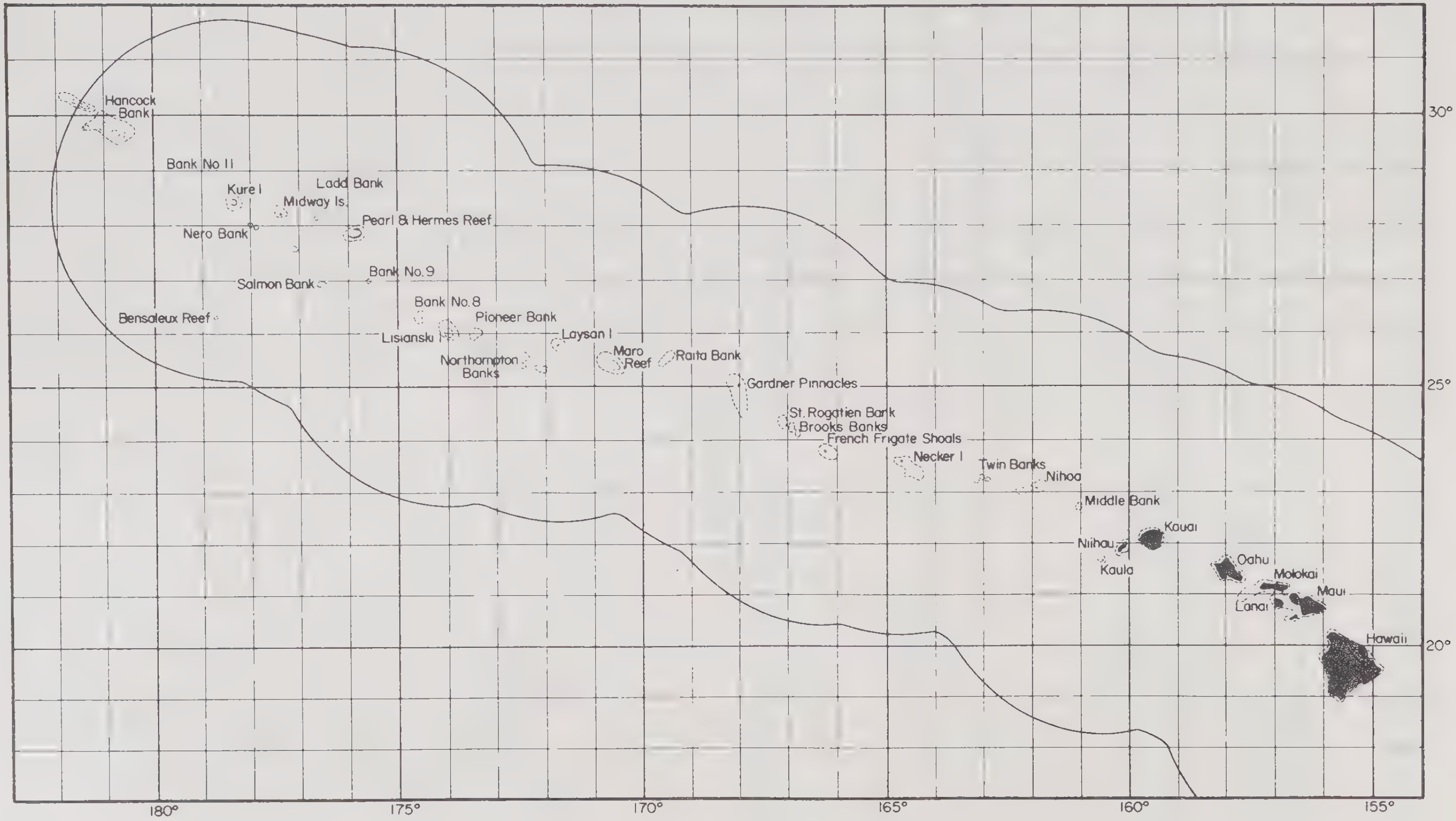
The range of ehu is limited to the Indo-western Pacific, and within this region the distribution is considered discontinuous and is restricted to the Indian Ocean, southern Japan, and Polynesia (Druzhinin, 1970; Forster et al., 1970). Within the Hawaiian Islands ehu is caught on nearly every major bank from the island of Hawaii to Kure Atoll (Figure 1). Their major habitat is the bottom in areas of deep (200 to 350 m) dropoffs around ledges, rock outcrops, and pinnacles (Ralston and Polovina, 1982). During the sampling period they were most abundant in the area northwest of Lisianski bank (see paper in this proceedings by Uchiyama and Tagami), comprising 45 to 86 percent of the total number of bottomfishes caught. Ehu is a very important food fish in Hawaii and is of high commercial value (Uchida et al., 1979).

The major objectives of this study were to determine the spawning season, size at first maturity, and sex ratio of ehu and to determine any differences in these aspects of spawning among banks within the NWHI chain. All of this information is important for any future management of the fishery.

METHODS

Fish were sampled during cruises of the NOAA ship Townsend Cromwell over a 5-year period between 1977 and 1981. The majority of fish were caught at bottom handline fishing stations at depths ranging from 200 to 350 m from various banks within the NWHI throughout the year (Figure 1). Hydraulic handline gurdies were used usually with four Nos. 20 or 28 hooks. Stripped squid were used as bait. Of the 935 ehu caught at these stations, 273 (33 percent) were males and 553 (67 percent) were females; 109 fish were not sexed. All fish were weighed to the nearest 0.01 kg and measured to the nearest 0.1 cm. About 300 ovaries collected during fishing operations were either frozen or preserved in 10 percent Formalin. Testes were not saved. Ovarian samples were taken randomly on each cruise and were not necessarily representative of any area, size class, developmental stage, or time of year.

To evaluate differences in ehu reproduction within geographic locations in the NWHI, the area was divided into three different regions. Region I extended from Nihoa to Gardner



Hancock Bank
Bank No 11
Kure I
Ladd Bank
Midway Is.
Pearl & Hermes Reef
Nero Bank
Salmon Bank
Bank No. 9
Bank No. 8
Bensaleux Reef
Pioneer Bank
Lisianski I
Laysan I
Northampton Banks
Maro Reef
Raita Bank
Gardner Pinnacles
St. Rogatien Bank
Brooks Banks
French Frigate Shoals
Necker I
Twin Banks
Nihoa
Middle Bank
Kauai
Niihau
Kaula
Oahu
Molokai
Maui
Lanai
Hawaii
30°
25°
20°
180°
175°
170°
165°
160°
155°

Figure 1. The Hawaiian Islands

Pinnacles, region II from Raita Bank to Lisianski Island, and region III from Pearl and Hermes Atoll to Kure Atoll (Moffitt, 1980).

Various methods have been used to define the spawning season in fishes. The main criterion used in the past has been to monitor the development of the ova, determined by ovum diameters, throughout the year. Each mode in the frequency distribution of ovum diameters was assumed to represent a distinct developmental stage. This technique was used successfully by Clark (1934) for the California sardine, Yuen (1955) for bigeye tuna, and Otsu and Uchida (1959) for albacore. Another method used was to note the developmental stage by microscopically examining the physical characteristics of individual ovum. This can be accomplished by taking a sample from an ovary and teasing out the ova (Uchiyama and Shomura, 1974) or by histologically examining a section of the ovary (Crossland, 1977). The gonadal somatic index (GSI) may also be calculated to assess the fluctuations in ovary weight as a function of body weight during the year (Bagenal and Braum, 1968; Morse, 1980; Goldberg, 1981; Love and Westphal, 1981; Baglin, 1982). A combination of these methods that allowed for a rapid assessment of maturity state and spawning frequency were used.

Each preserved pair of ovaries was blotted dry and weighed to the nearest 0.1 g. To determine stages of development, a dorsoventral sample (completely through the ovary) was taken at the posterior half of the left lobe with a cork borer. The entire sample was teased apart to separate the ova from ovarian connective tissue. All of the ova within the sample were examined under a compound microscope at 40X magnification. The proportion of ova in each development stage and the most advanced stage was noted. Random ovum diameters were measured to determine the size range in each stage, as well as the largest ovum in each sample. The stage of development was classified according to physical characteristics not necessarily dependent on ovum diameters (Uchiyama and Shomura, 1974) (Table 1).

Fecundity was estimated from five ripe-appearing ovaries that were frozen at the time of collection. Thawed samples were placed in modified Gilson's solution (Bagenal and Braum, 1968), until the ova were freed from connective tissue following the procedure described by Kikkawa and Everson (see report in this proceedings). The diameter of 100 randomly selected ova was measured from each ovary (Clark, 1934; Yuen, 1955) to determine the most advanced mode. Ova in this modal group were counted to obtain fecundity estimates since they are most likely to be spawned in a season. These may include ova from maturity stages III to VI. Subsamples were obtained using Van Dalsen's (1977) volumetric technique, modified slightly by Kikkawa and Everson (see report in this proceedings). The ova were placed in a 2,000-ml beaker and initially mixed with a stirring rod. To create a counterflow a magnetic stirrer was then switched on until a homogeneous mixture was obtained. At this time a 5-ml

TABLE 1. DESCRIPTION OF REPRODUCTIVE STAGES OF EHU BASED ON EXTERNAL APPEARANCE OF OVARY AND MICROSCOPIC EXAMINATION OF OVA

Maturity Stage	External Appearance of Ovary
I. Primordial (diameter 0.04 to 0.13 mm) Oocytes are transparent and irregular in shape with no sign of vitillogenesis. These comprise the oocytes from which smaller numbers of ova mature. Individual ovum are invisible to the naked eye and very difficult to separate from connective tissue.	1. Immature Ovaries are small and firm in texture and ribbonlike in shape. Very light (white) in color. Sex may be discernible by gross examination. Individual ova are not visible.
II. Early developing (0.10 to 0.16 mm) Oocytes are semitransparent and ovoid in shape. A chorian membrane has begun to form around the ovum and yolk granules have started to be deposited within. Barely discernible to the naked eye.	
III. Developing (0.26 to 0.52 mm) Ova are spherical in shape and have become completely opaque and yellow due to yolk material. They are readily visible within the follicles and can be separated from connective tissue fairly easily.	2. Developing Ovaries enlarged, elongated, and slightly swollen in girth. Individual ova discernible through the ovarian membrane. Ova, visible to the eye, are small, white, and granular. Ovary appears yellow due to the presence of yolk material.
IV. Advanced developing (0.39 to 0.52 mm) A translucent margin bordered by a fertilization membrane is visible. Oil droplets are just starting to form.	
V. Early ripe (0.44 to 0.58 mm) Oil droplets have begun to cluster into a single oil globule. The yolk material appears translucent, and ova have become completely round.	3. Ripe Ovary is greatly enlarged reaching its maximum size as it fills the abdominal cavity and hydration takes place. Large ripe ova are discernible through the thin ovarian membrane; ova are easily dislodged from follicles and connective tissue. Ovary is yellow to orange in color.
VI. Ripe (0.5 to 0.78 mm) Ova have become almost completely transparent. A single, pronounced yellow oil globule has formed. Ovary wall has become considerably thinner, oil globule (diameter 0.13 to 0.2 mm).	
VII. Residual (atretic) Ova have become shrunken, wrinkled, and translucent in appearance. Degeneration and resorption in progress.	4. Spent Ovary empty, flaccid in appearance, and dark gray in color — only primordial ova left. Ovary wall very thick and tough. Residual oocytes may be present.

sample was drawn. This procedure was repeated for each ovary examined. Fecundity estimates were obtained from the formula

$$F = \frac{1}{2} (N_1 + N_2) \left(\frac{V}{5 \text{ ml}}\right)$$

where

F = fecundity
N_1 and N_2 = number of ova in each subsample
V = total volume of the mixture in milliliters

RESULTS

Seasonality of Spawning

Stages of maturity, based on the physical characteristics of the ova, were compared with GSI calculated for ehu captured at various times throughout the year. The GSI increased with advancing stage of maturity and was highest at stage VI (ripe stage). The GSI and stages of maturity were positively correlated ($r = 0.8562$, $N = 286$, $P < 0.01$) (Figure 2). A plot of the mean GSI by month (data for all years pooled) (Figure 3) showed a similar trend when compared with the percentage frequency of maturity stage versus month (Figure 4). The mean GSI values were relatively low from January to April when females were exclusively in stages I and II. In May-June, however, as evidenced by the mean GSI and maturity stages, maturing females were more prominent in the samples. The highest mean GSI's and the most advanced maturity stages were found in July-September. The GSI values decreased and the number of advanced stages declined sharply in October and remained low the rest of the year. Based on these results, the spawning season can be divided into four separate phases: resting phase (January-April), maturing phase (May-June), spawning phase (July-September), and postspawning or recovering phase (October-December). Similar results were obtained when monthly mean GSI's were compared for each individual year from 1977 to 1981.

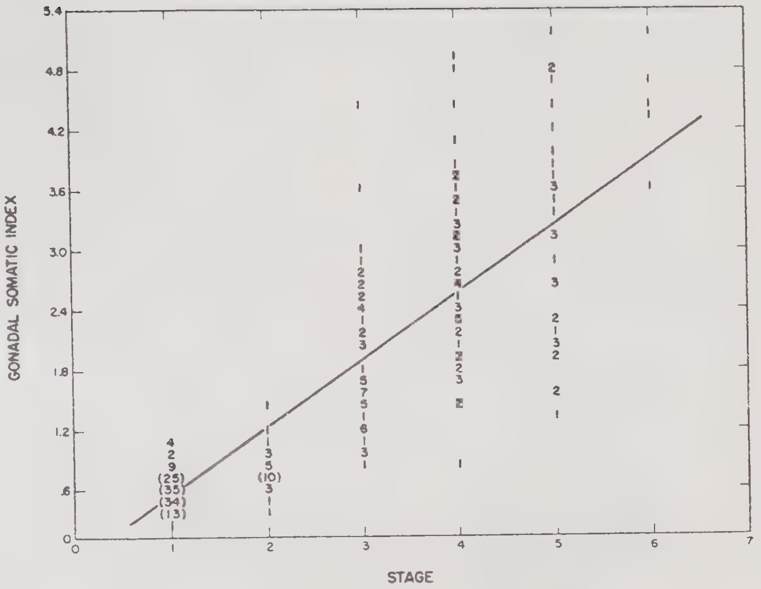


Figure 2. The relationship of gonadal somatic index and maturity stages (I-VI) for 286 ehu ovaries collected between 1977 and 1981.
$Y = 0.67422x - 0.2355$
$r = 0.8562$

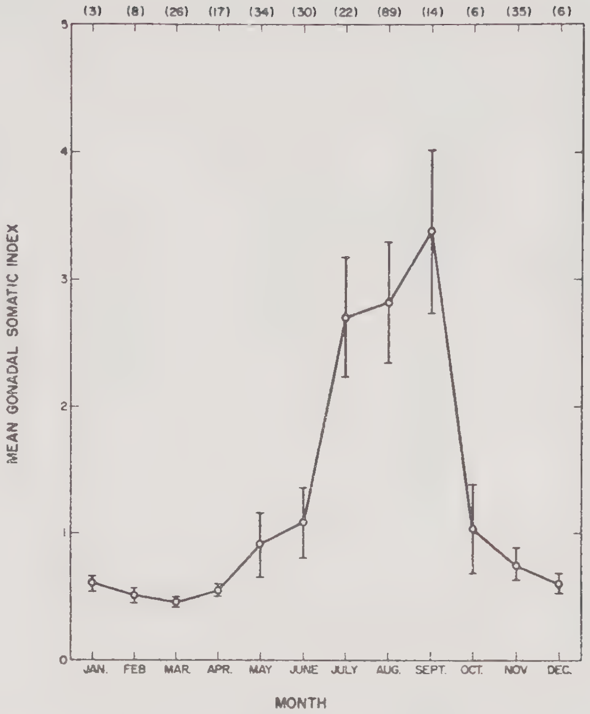


Figure 3. Monthly mean gonadal somatic index for 286 ehu collected between 1977 and 1981. Vertical lines indicate 95 percent confidence limits.
(N) = Number of samples per month

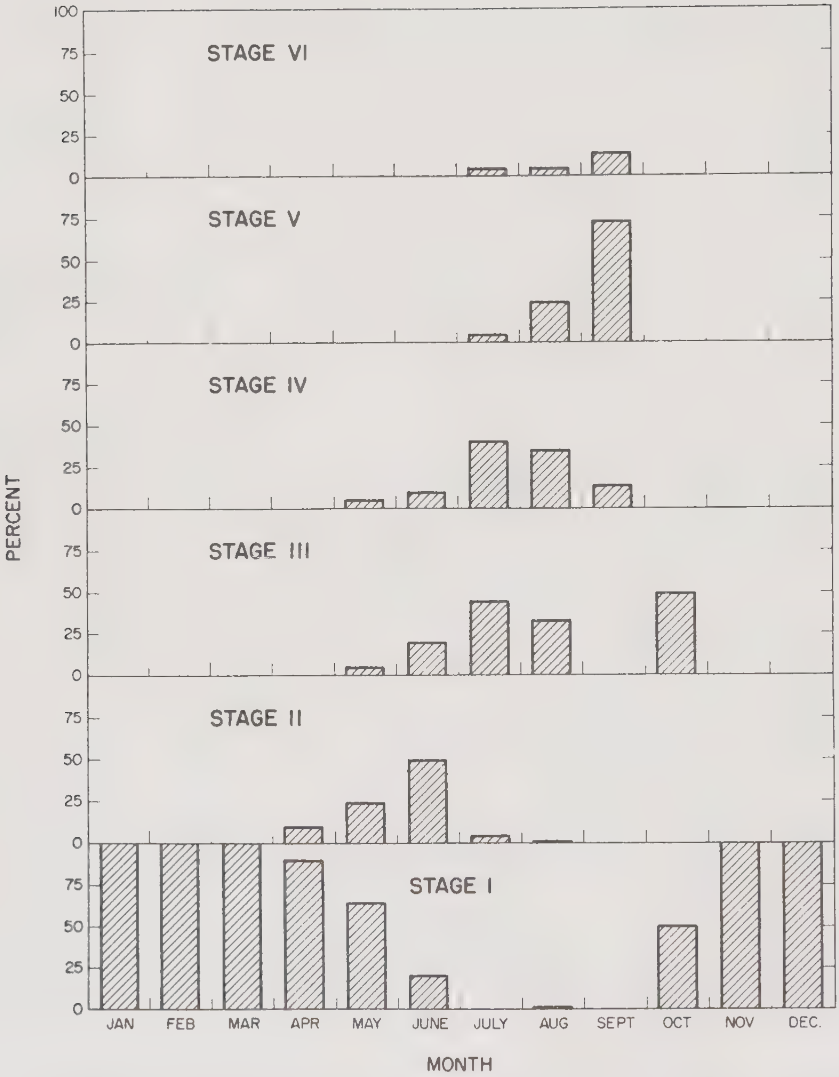


Figure 4. Monthly percentage of ehu ovaries in various stages of maturity, 1977-81

The presence of residual ova (Table 2) was highest (37 percent) in the postspawning phase of maturity and lowest in the maturing phase (3.4 percent).

TABLE 2. OCCURRENCE OF RESIDUAL OVA BY MONTH FOR EHU OVARIES 1977-81. MATURITY STAGES I to V OF DEVELOPING OVA ARE ALSO NOTED FOR EACH OVARY.

Month	Stage	Number	Percent
January	I	1	1.7
February	I	5	8.5
March	I	8	13.6
April	I	7	11.9
May	I	2	3.4
June	--	--	--
July	III	3	5.1
August	III, IV, V	8	13.6
September	--	--	--
October	I	2	3.4
November	I	19	32.2
December	I	2	3.4

Ova diameters were compared with maturity stage for five ovaries in different stages of development. Ova size increased with each advancing stage of development (Figure 5).

The results show that ehu may be multiple spawners and may release several batches of ova during a season. Evidence for multiple spawning is the presence of multiple modes in the ova diameter frequency distribution (Figure 6). Additionally, mature ovaries found during the spawning season contained residual ova (Table 2), and no ehu were found with ovaries that were completely spawned out (containing only stage I ova) until the end of the spawning season.

Maturation

Two separate criteria were evaluated to determine the relationship between maturity and size of fish. In this study, mature fish are defined as those with ovaries that contain developing (stage III) ova and have the potential to spawn during the current season. In contrast, ripe fish are defined as those with ovaries containing ripe (transparent - stages V, VI) ova and are considered imminent spawners with at least one batch spawned during the current season.

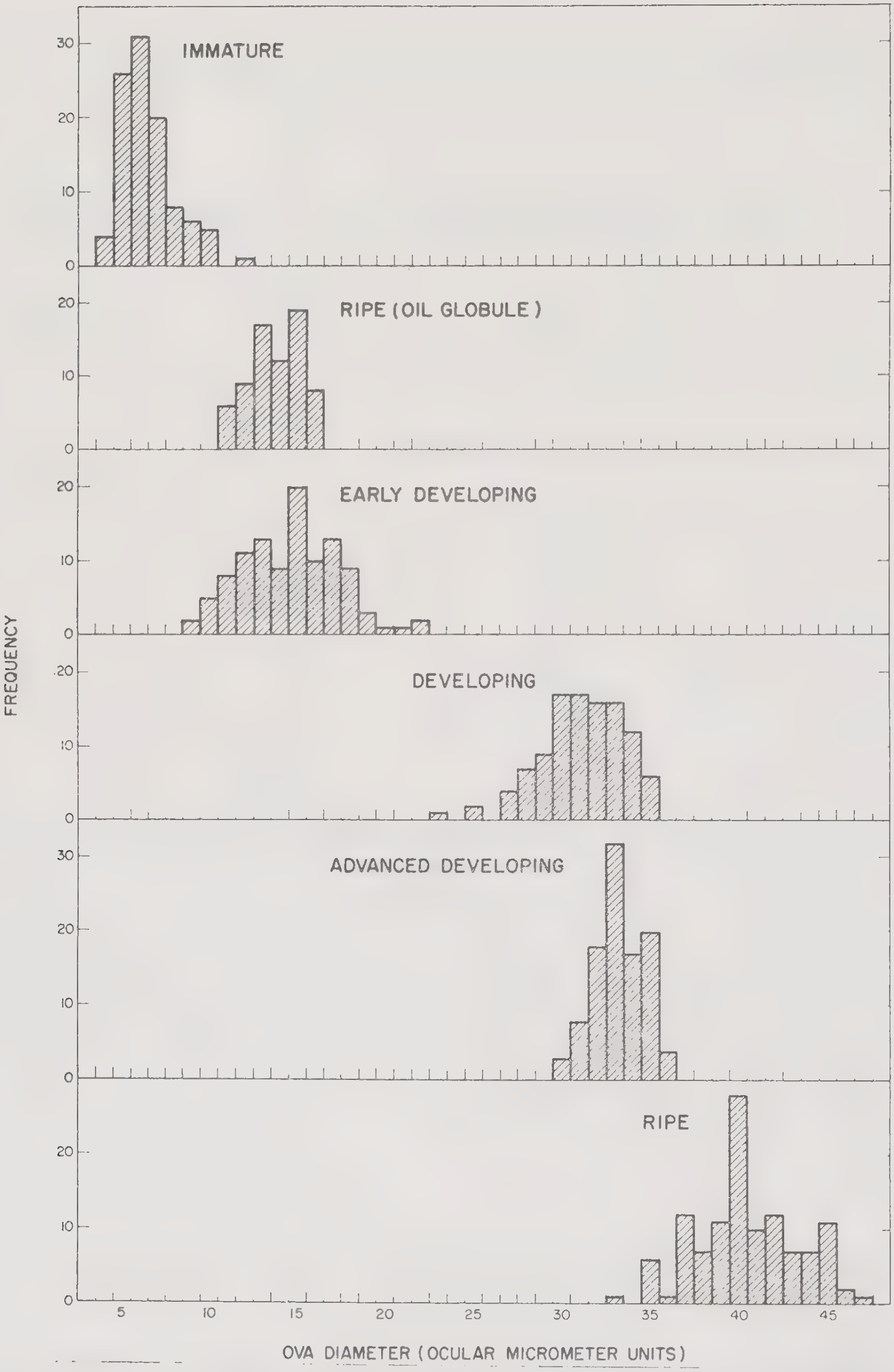


Figure 5. Ova diameter frequency distribution of the most advanced ova for five ehu in various developmental stages. Also shown is the size (diameter) frequency distribution of the oil globule in ripe ova. 1 mm = 72.5 ocular micrometer units

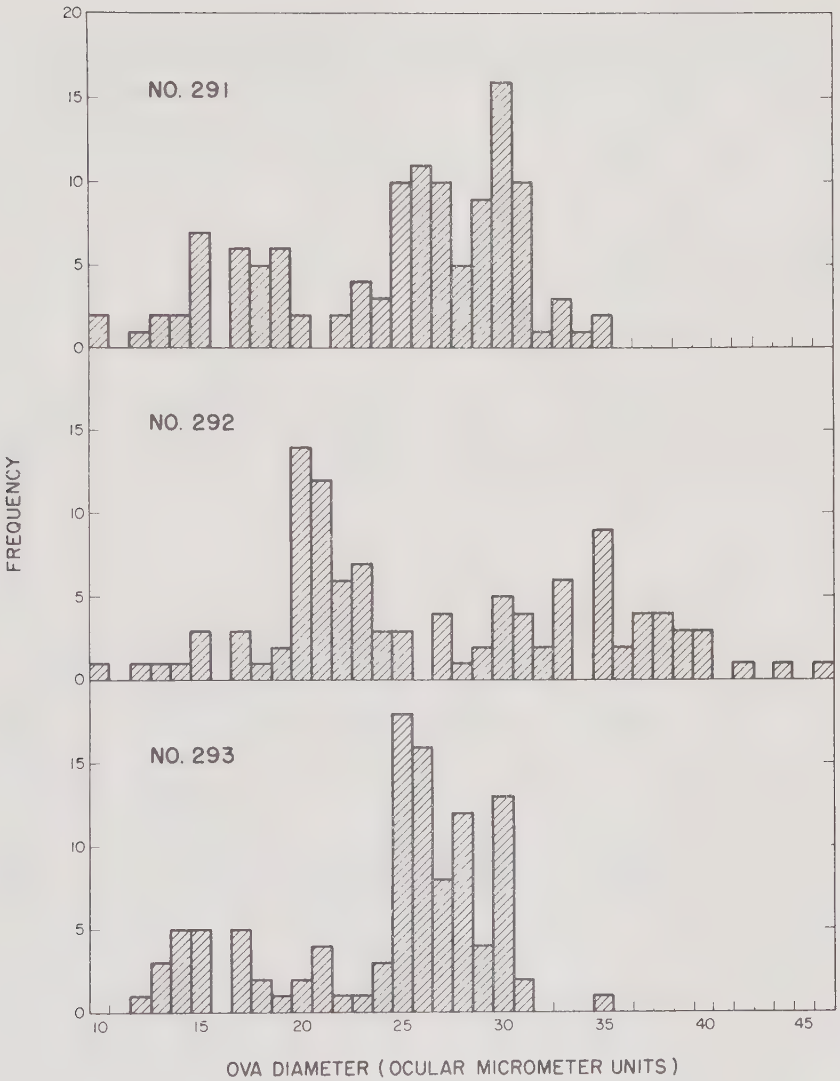


Figure 6. Ova diameter distribution in three ehu ovaries used in fecundity estimates. 1 mm = 72.5 ocular micrometer units

In May, 12 percent of the ehu were mature (Table 3); mature ehu increased to 95 percent by July. The fish captured from May to September ranged from 29.7 to 63.5-cm fork length (FL). Of these, the smallest fish considered mature was 29.8 cm. The proportion of mature fish in each 5-cm size class by month showed that 50 percent were mature in the 25 to 30-cm size class. The proportion increased sharply to 86 percent at 30 to 35 cm, then remained fairly stable through the rest of the size classes.

TABLE 3. THE PERCENTAGE OF MATURE (STAGES III TO VI) AND RIPE (STAGES V TO VI) EHU OVARIES BY FISH SIZE (FL) FOR EACH MONTH OF THE SPAWNING SEASON

Size Class	May	June	July	August	September	Total
25 - 30						
N	1	--	1	--	--	2
% M	0	--	100	--	--	50
% R	0	--	0	--	--	0
30 - 35						
N	--	1	1	5	--	7
% M	--	0	100	100	--	86
% R	--	0	0	33	--	33
35 - 40						
N	3	1	5	13	--	22
% M	0	0	80	100	--	77
% R	0	0	0	23	--	23
40 - 45						
N	7	6	5	19	--	37
% M	0	50	100	90	--	68
% R	0	0	0	26	--	13
45 - 50						
N	12	6	4	21	4	47
% M	17	50	100	90	100	68
% R	0	0	25	24	75	19
50 - 55						
N	4	9	2	21	2	38
% M	0	22	100	100	100	71
% R	0	0	0	24	100	18
55 - 60						
N	6	6	1	7	6	26
% M	33	17	100	100	100	65
% R	0	0	0	43	83	31
60 - 65						
N	--	1	1	--	2	4
% M	--	0	100	--	100	75
% R	--	0	100	--	100	75
Total						
N	33	30	22	86	14	185
% M	12	30	90	98	100	71
% R	0	0	9	27	86	20

Due to the limited number of samples at the lower size classes, it was difficult to determine the smallest size at which ehu reach sexual maturity. The available data indicate that at least some of the females are mature at 25 to 30 cm for age I (Uchiyama et al., in preparation) and that the majority are mature by the time they reach 35 to 40 cm or age II.

Ripeness as an indication of maturity showed a slightly different trend with size (Table 3). There were no ripe fish in the 25 to 30-cm range; the smallest fish with ripe ovaries was 31.8 cm; however, the small sample size at the lower end of the range may bias the data. The 30 to 35-cm range showed a 33 percent increase in the number of ripe fish. In July, 9 percent of the ehu had ripe-appearing ova and no fish <45 cm was ripe. By August, small (<45 cm) ripe fish began to appear and the number of ripe to nonripe increased to 27 percent. In September, 86 percent of all fish caught were ripe, but fish <45 cm were not represented.

Sex Ratio

Sex ratio was determined from a total of 833 ehu collected over a 5-year period. The overall ratio for the period between 1977-81 deviated significantly from the expected 1:1; 557 (66.9 percent) were female and 276 (33.1 percent) were male. Each separate year also showed a significant deviation from 1:1. The sex ratio, calculated for each 5-cm size class, showed that for small ehu (25 to 30 cm), the female to male ratio was 1:1, but among larger (older) fish, there was a gradual increase in the percentage of females. The percentage of females in the 45 to 50-cm class was 65 percent, 84 percent in the 50 to 55-cm class, and 96 percent in the 55 to 60-cm class (Table 4). Contingency table analysis showed that sex ratio and size are not independent (χ^2 $P < 0.05$, d.f. = 7). An analysis of the difference in sex ratio for October and May to test for possible variation due to behavioral factors such as spawning aggregation or female feeding dominance showed no significant difference (Table 5). During the spawning months, however, the percentage of males in the sample dropped from 41 percent in June to 18 percent in August, rose slightly to 26 percent in September, before approaching near normal levels (for this population of ehu) of 38 percent in October. This suggests that sex ratio and season are also dependent (χ^2 $P < 0.01$).

TABLE 4. TEST TO DETERMINE THE DEPARTURE OF THE SEX RATIO OF EHU FROM 1:1 BY 5-CM FL INTERVALS. (DATA POOLED OVER 5 YEARS)

Fork Length (cm)	N	Females (%)	χ^2
25 - 30	12	50.0	0
30 - 35	48	45.8	0.33
35 - 40	114	59.6	4.24*
40 - 45	211	53.6	1.07
45 - 50	199	65.3	18.70*
50 - 55	162	84.0	74.68*
55 - 60	74	96.0	62.48*
60 - 65	10	90.0	6.40*

*$P < 0.05$

TABLE 5. TESTS OF THE HYPOTHESIS THAT SEX RATIO DID NOT VARY SIGNIFICANTLY WITHIN MONTHS OF THE YEAR FROM THAT OF THE ACTUAL POPULATION OF EHU (2:1)

Month	N	Females (%)	Contribution to Total χ^2
January	33	60.6	0.6
February	33	69.7	0.1
March	59	55.9	3.2
April	96	69.8	0.3
May	57	68.4	0
June	176	58.5	5.5
July	50	62.0	0.6
August	138	81.9	14.1
September	57	73.7	1.2
October	21	61.9	0.3
November	96	63.5	0.5
December	17	70.6	0.1

Note: Total $\chi^2 = 26.50$, d.f. = 11, $P < 0.01$

Fecundity

A linear regression using natural log transformed data provided the best fit when fecundity (F) was compared with fork length (FL) in centimeters and total body weight (W) in kilograms. The regression equations were $F = 0.05413\ (FL)^{4.32}$ and

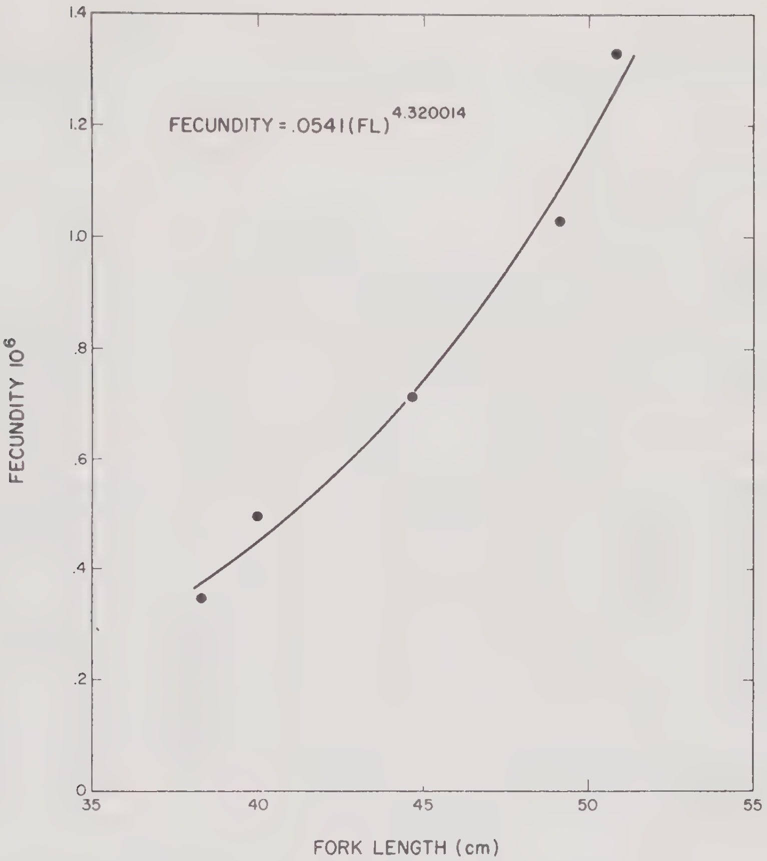


Figure 7. Length-fecundity relationship of ehu

$F = 3.412 \times 10^5 (W)^{1.38}$. This indicated that fecundity increased as a function of both length ($r = 0.991$) and weight ($r = 0.987$) (Figure 7). Because of the sample size ($N = 5$), the estimates of fecundity should be considered tentative, although the correlation for both indicators was quite high. The data did give an approximation of the number of ova spawned by a particular size range of fish. The estimated fecundity ranged from 349,600 to 1,325,600 for ehu between 38.3 and 50.8-cm FL and between 0.97 and 2.49 kg.

Regional Comparisons

To test for differences in spawning season among the three regions within the NWHI, monthly mean GSI versus region was compared. All three regions showed a similar trend of low GSI in January-June, increasing in July-September, then decreasing in October-December. The available data did not show any significant differences in monthly mean GSI among regions.

The sex ratio in regions 1 and 3 did not differ from that of the population ratio (2:1) whereas in region 2 the ratio was slightly skewed in favor of females (2.8:1).

DISCUSSION

Spawning Seasonality

Ehu begin maturing throughout the NWHI in May and spawn in July-September. This corresponds to the time of year when environmental conditions such as temperature and photoperiod are at a peak in this area (Uchida, 1977). Similar observations were made by Grimes and Huntsman (1980) on the vermilion snapper, *Rhomboplites aurorubens*, of North and South Carolina, by Crossland (1977) on the porgy, *Chrysophrys auratus*, in the Hauraki Gulf, and by Ralston (1981) for opakapaka, *Pristipomoides filamentosus*, in Hawaii. All of these investigators found snappers to be summer spawners. Ehu seem to have a shorter, more defined spawning season than many other snappers. Druzhinin (1970) reported that the spawning period of lutjanids may be very protracted, extending over a period of several months. In contrast, ehu in spawning condition were found only during a 3-month period. Spawning ceased in October when GSI values dropped and ovaries containing ripe ova were no longer found. Further degeneration takes place in November-December as indicated by a high percentage of residual ova in the ovaries during this period. Goldberg (1981) found atretic ova near the close of the spawning period when the ova that failed to complete yolk deposition underwent resorption.

Ehu appear to be serial spawners, that is, they release multiple batches of ova during the season. The actual mechanism for this type of spawning varies considerably among different species and depends to a large degree on the environmental conditions. In the Japanese horsemackerel, *Trachurus japonicus*, a dominant egg batch is spawned in the most favorable breeding period, then smaller batches are spawned under less favorable environmental conditions (Chigirinskiy, 1970). Crossland (1977) reported similar results in which serial spawning took place on an annual cycle where successive batches of ripe eggs matured from a stock of developing eggs. Results of this study indicate that a similar pattern occurs with ehu where a developing group of ova matures each year from a core of primary ova and various batches of ova ripen and are spawned each season from this developing stock. Further evidence of serial spawning is that spawned-out ovaries containing mainly primordial ova were not found until the end of the spawning season. This observation was also made for the black croaker, *Cheilotrema saturnum* (Goldberg, 1981). In addition, ehu ovaries contained ova in various stages of development throughout the spawning season, supporting the contention of Grimes and Huntsman (1980) that this may also indicate fractional spawning.

It can be concluded that ehu ovaries develop asynchronously (Wallace and Selman, 1981) throughout the year, but during the maturation phase they develop synchronously and batches of ova ripen and are spawned. The final stage, that is, from ripe to actual spawning, occurs very rapidly (Grimes and Huntsman, 1980), as evidenced by paucity of ripe females and the complete absence of hydrated ovaries in the samples. The absence of fish with ripe or hydrated ova may also be due to behavioral factors, i.e., fish feed less prior to spawning (Reshetnikov and Claro, 1976) or that running ripe fish may shed their eggs when lifted out of the water (Htun-Han, 1978). The latter explanation is very pertinent to ehu since they are caught in deep water and often experience severe stress from the change in pressure as they are brought to the surface.

Investigators have used various criteria to determine the minimum size of sexual maturity. Many feel that the presence of developing (type III) ova indicates that the fish is likely to spawn during the current season (Clark, 1934; Crossland, 1977; DeMartini and Fountain, 1981). For ehu, the presence of ripe (types V and VI) ova gave a better indication of the percentage of fish that will actually spawn in any size class. Ehu with mature (type III) ovaries began appearing in May and were always found in greater proportion than those with ripe ovaries. These fish have the potential to spawn, but many never reach the ripe stage due to environmental conditions (Chigirinskiy, 1970) or age constraints (Clark, 1934). The ova that did not mature would cease development and be resorbed. As with other snappers (Starck and Schroeder, 1971; Grimes and Huntsman, 1980) larger ehu (>45 cm) mature earlier in the season and remained in spawning condition longer than small (<45 cm) fish.

The smallest mature ehu caught was 29.8 cm, and 50 percent of the fish in the 25 to 30-cm size class had mature ovaries. In contrast, the smallest fish that had ripe ovaries was 31.8 cm, and 33 percent in the 30 to 35-cm size class were ripe. Because of the scarcity of small size classes, due possibly to hook selectivity (Ralston, 1982) or other behavioral factors, size at maturity could not be confidently estimated. The data indicated, however, that some ehu spawn during their first year at around 32 cm and that the majority spawn after age II (39 cm).

There appeared to be no differences in spawning season, maturation, and sex ratio for the three regions within the study area. Apparently the change in the environment accompanying the change in latitude from Nihoa to Midway Islands is not significant enough to cause any fluctuation in the spawning within the NWHI.

Sex Ratio

The sex ratio of ehu (all samples pooled) deviated significantly from the expected 1:1 and also by size and season. There was a preponderance of females in nearly every category. A deviation in sex ratio among different size classes was also found in the vermilion snapper (Grimes and Huntsman, 1980). Female vermilion snapper increased to 60 percent of the sample at 25 to 30-cm total length (TL), to 70 percent at 50 to 55 cm, and to 90 percent above 55 cm, suggesting that this anomaly resulted from differential mortality and longevity. The data for ehu show an even greater disproportion of females in the upper size range (Table 5). This implies greater male mortality in the higher (>30 cm) size classes. Age and growth data for ehu are very limited; however, female Lutjanus synagris grow more rapidly and survive to a greater age than males (Reshetnikov and Claro, 1976).

The data for the sex ratio of ehu over the year show that, during the prespawning month of June, the ratio of males increases to about 41 percent then decreases to 18 percent during the peak spawning period in August (Table 4). This suggests behavioral changes during the spawning season such as feeding response and spawning aggregations by females.

Fecundity

Estimates of fecundity for ehu are slightly higher than those for the vermilion snapper. Estimates of the fecundity of vermilion snapper ranged from 8,168 to 1,789,998 ova for 41 females 229 to 557-mm TL (Grimes and Huntsman, 1980). The estimates for ehu ranged from 349,000 to 1,325,600 for fish between 38.3 and 50.8 cm and are based on the total number of eggs that may be spawned under ideal environmental conditions in a given season.

Because ehu is a multiple spawner, the estimates may be less precise since it is difficult to determine the number of spawnings per year and the number of eggs per spawning (Hunter and Goldberg, 1980). Environmental conditions may determine whether some or all of the batches may be spawned (Chigirinskiy, 1970). Also, the relationship among the number of maturing ova in an ovary, the number of ova spawned, and the viable larvae produced are unknown. Therefore, considering all these factors, fecundity estimates for ehu represent an approximation of its reproductive potential.

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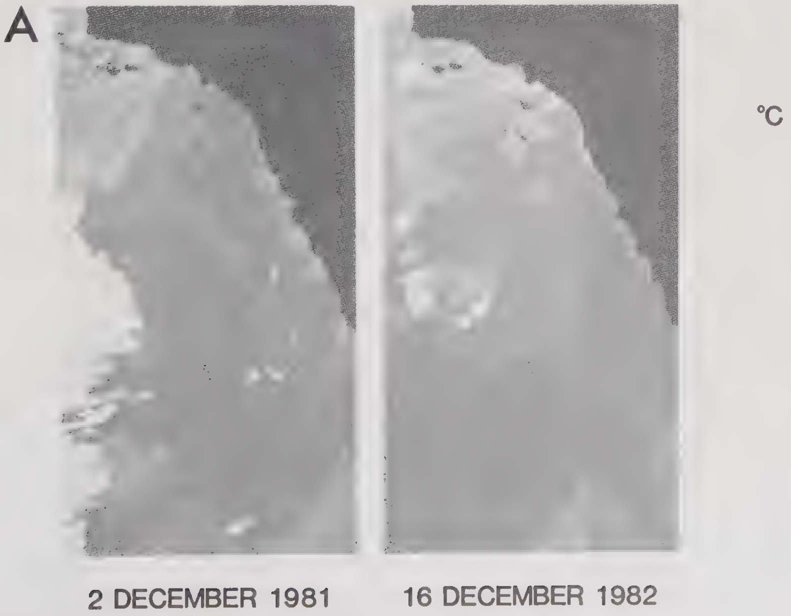
Satellite Observations of the 1982–1983 El Niño Along the U.S. Pacific Coast

Abstract. *Satellite infrared temperature images illustrate several effects of the 1982–1983 El Niño: warm sea-surface temperatures with the greatest anomalies near the coast, weakened coastal upwelling, and changes in surface circulation patterns. Phytoplankton pigment images from the Coastal Zone Color Scanner indicate reduced productivity during El Niño, apparently related to the weakened coastal upwelling. The satellite images provide direct evidence of mesoscale changes associated with the oceanwide El Niño event.*

The El Niño event that has caused major physical and biological changes in the equatorial Pacific since early 1982 began to affect the waters off California by December. Changes in surface and subsurface temperature, sea level, surface currents, and plankton have been noted (*1*, *2*). Oceanographic data obtained fortuitously on previously scheduled cruises, at shore stations, or from sampling programs initiated in haste after the event had been recognized are limited in spatial and temporal coverage. Global sea-surface temperature (SST) data analyzed routinely by the National Oceanic and Atmospheric Administration (NOAA) (*3*) provide good coverage, but only after averaging over large areas has removed energetic mesoscale features.

Fortunately, systematic sampling of the ocean surface has been carried out with a variety of sensors aboard orbiting satellites during the entire course of the



2 DECEMBER 1981   16 DECEMBER 1982

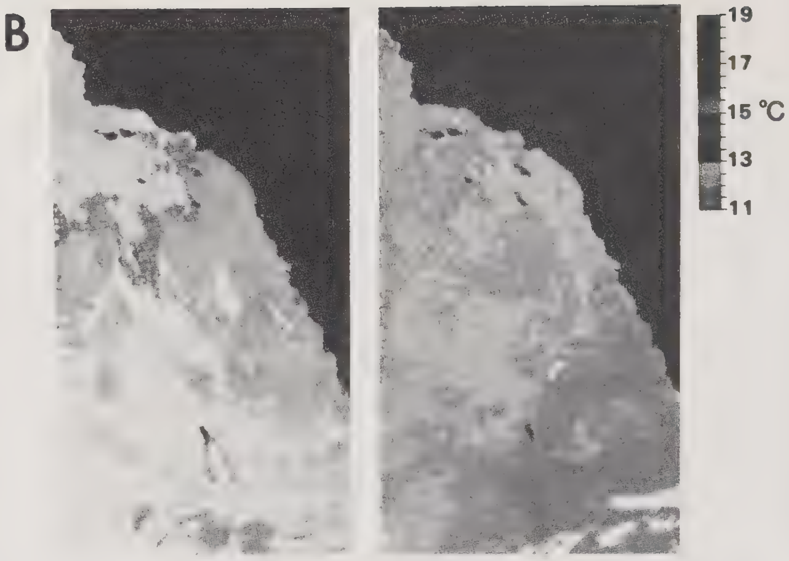
Fig. 1A. Advanced Very High Resolution Radiometer sea-surface temperature image off southern California.

1982–1983 El Niño. These sensors provide extensive and synoptic coverage with resolution to 1 km^2. Accurate estimates of SST can be retrieved from Advanced Very High Resolution Radiometer (AVHRR) infrared radiance data with sufficient precision to permit the detection of interannual changes. Satellite imagery of the SST field reveals changes in coastal upwelling intensity and circulation patterns, as well as gross SST anomalies.

The AVHRR data from daytime NOAA-7 passes (~ 1430 local time) were received and processed at Scripps Institution of Oceanography's Satellite Oceanography Facility. Calibration and multichannel SST retrieval were based on established and verified algorithms (*4*). The differential effect of water vapor in thermal-infrared channels 4 and 5 allows correction of the negative error caused by atmospheric absorption and reemission of infrared radiation from the sea surface. The matching of satellite SST estimates from 18 February 1982 with ship SST measurements from 35 stations off southern California occupied on the same day (*5*) yielded a root-mean-square deviation of ± 0.35°C with a negligible bias of +0.07°C.

On 16 December 1982, the ocean off the coast of southern California and northern Baja California was not consistently warmer than 1 year earlier (Fig. 1A): the mean and standard deviation of pixel-by-pixel SST differences were −0.44° ± 0.89°C. However, striking differences in mesoscale features are apparent. The plume of cold water off Point Conception (top left corner) is a perennial feature formed by offshore advection of California Current water from the north augmented by coastal upwelling. The plume was still present in December 1982 but was warmer by up to 3°C than in 1981. Small patches of relatively cool water along the coast were less intense in December 1982, a sign of weakened coastal upwelling.

On 10 January 1983, this region was considerably warmer than 1 year earlier (Fig. 1B). Pixel-by-pixel differences averaged +1.72° ± 1.20°C and were greater than +4°C near the coast. Neither the plume of cold water off Point Conception nor signs of coastal upwelling were evident. However, cooler California Current water was present offshore and to the north just beyond the corner of the image. February satellite data show that the following effects of El Niño persisted: SST differences up to +4° to 5°C near the coast, very weak coastal upwelling, and no sign of a cold-water plume off Point Conception. An anomalously strong seasonal poleward countercurrent



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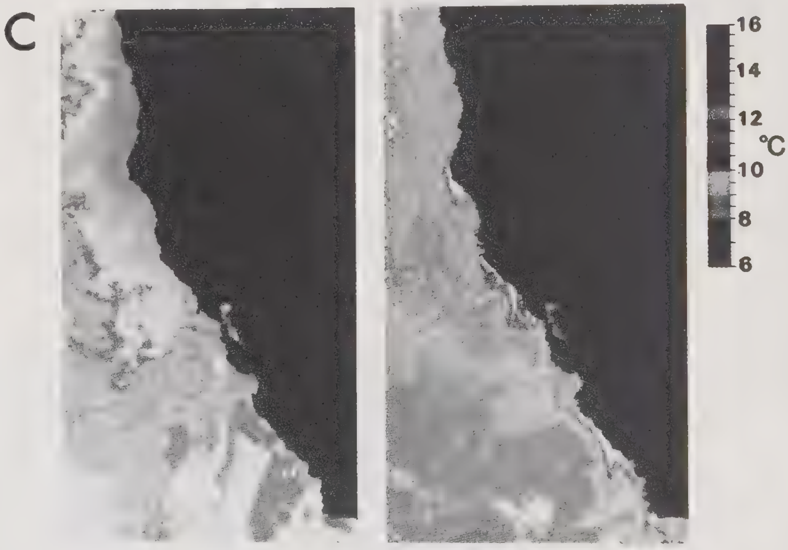

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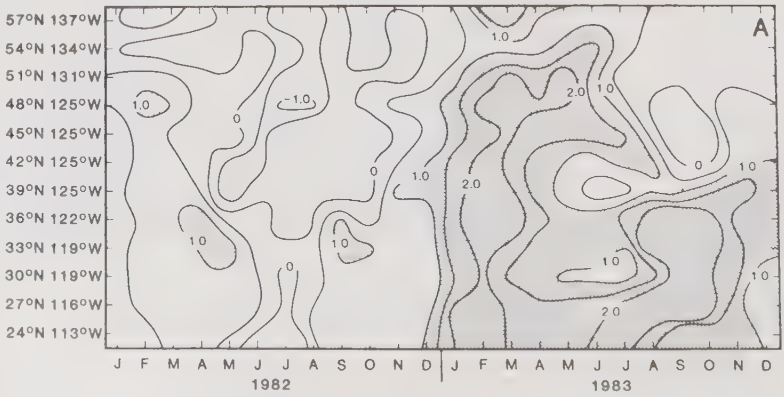

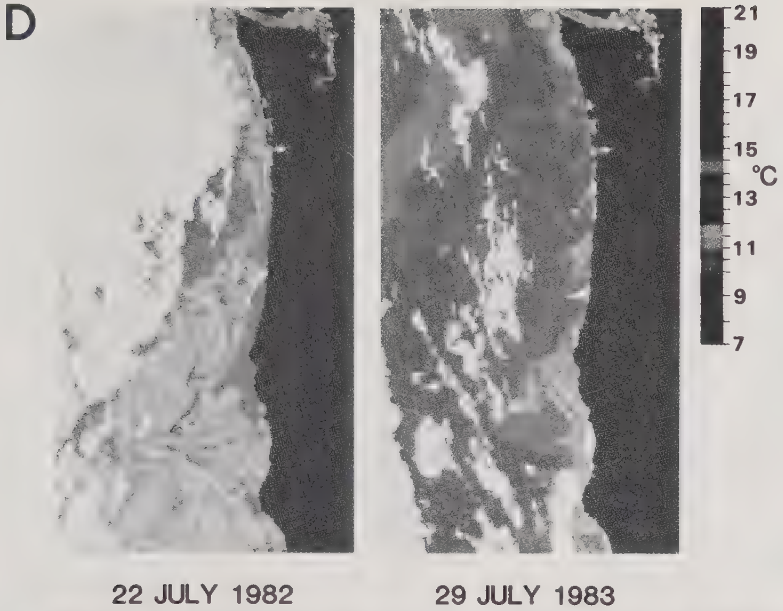

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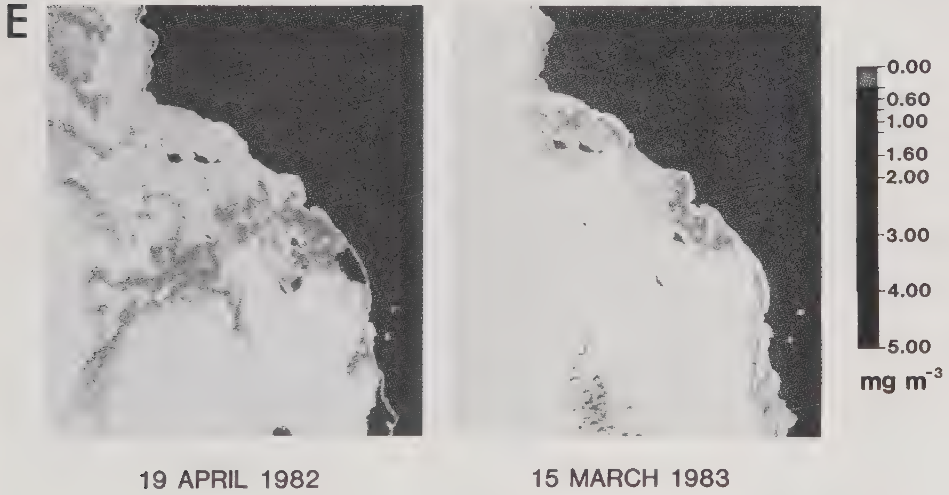

19 APRIL 1982

15 MARCH 1983

Fig. 1. Advanced Very High Resolution Radiometer sea-surface temperature images off southern California (B), central-northern California (C), and Oregon-Washington (D); Coastal Zone Color Scanner phytoplankton pigment images off southern California (E).

observed off Point Conception in February may account for the displacement of California Current water (*6*).

In April and May, effects of El Niño could not be seen in comparisons between 1982 and 1983 satellite images. During April and May 1982, SST anomalies of −0.3° to +2.2°C were observed off California (*3*), representing the "normal" interannual variability of the California Current system. An increase in coastal upwelling to near normal levels during April 1983 was indicated by cool water along the coast south of San Diego, California. By July 1983, however, the El Niño effects observed in December through February were once again evident: SST differences up to 4°C were associated with warm water intruding along the coast toward Point Conception, and coastal upwelling appears to have been distinctly weaker than in July 1982.

On 10 May 1983, the ocean off the coast of central and northern California was not uniformly warmer than 1 year earlier (Fig. 1C). Pixel-by-pixel differences were +1.58° ± 1.90°C and up to +5°C north of San Francisco. However, coastal upwelling south of San Francisco appears to have been more intense in 1983, when SST was colder by up to 4.5°C than in 1982. On 29 July 1983, the ocean off the coast of Washington and Oregon was much warmer than 1 year earlier (Fig. 1D). Pixel-by-pixel differences were +2.69° ± 1.99°C, with changes up to +6.7°C associated with weaker coastal upwelling.

The Coastal Zone Color Scanner (CZCS) on Nimbus-7 provides visible color data reflecting the biological effects of El Niño in terms of changes in phytoplankton biomass and productivity (*7*). On 15 March 1983, phytoplankton pig-

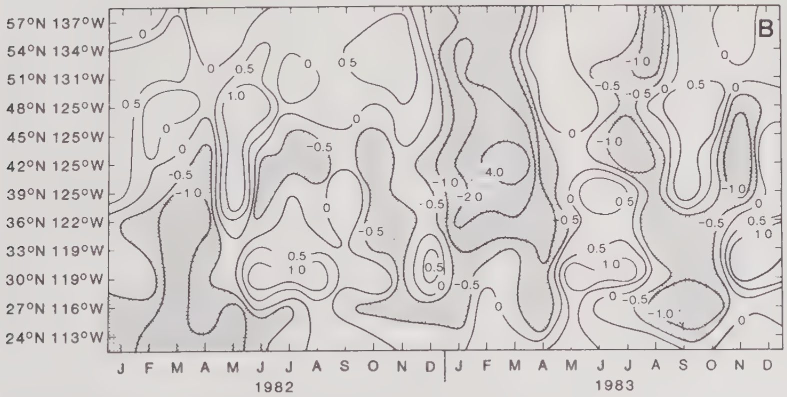

Fig. 2. Time series of 1982–1983 monthly anomalies along the Pacific coast. Monthly sea-surface temperature anomalies from 1942–1969 means (A) are from NOAA analyses of ship, buoy, and satellite data (*3*) averaged in 3° squares. Monthly upwelling index anomalies from 1946–1971 means (B) are normalized by the standard deviations of values published by Bakun (*13*). The upwelling index is equal to offshore Ekman transport, computed from surface wind stress vectors derived from synoptic analyses of the surface atmospheric pressure.

ment levels (C_{sat}) off southern California were considerably lower than on 19 April 1982 (Fig. 1E) (*8*). The 1983 C_{sat} values along the coast were generally less than half the 1982 values. In 1982, waters with $C_{sat} > 0.8$ mg m^{-3} extended more than 100 km offshore in plumes associated with upwelling near Point Conception. This represents typical early spring conditions in the Southern California Bight. In the 1983 image, only tenuous upwelling plumes can be seen at Point Conception, with high C_{sat} values only in nearshore waters. Monthly ship transects off southern California since March 1983 have shown increasing departures from normal: the maximum layer of chlorophyll deepened along with the mixed layer, and integrated chlorophyll values in the water column declined to one-quarter of the normal by August (*2, 9*). The satellite images suggest that the initial reduction of nearshore phytoplankton productivity during El Niño was associated with weakened upwelling.

These satellite data corroborate the results of two routine data analyses providing more complete spatiotemporal coverage of El Niño (summarized in Fig. 2). Along the coast from 27° to 49°N, markedly anomalous warm temperatures and weak upwelling indices began in December 1982 and peaked in February and March 1983 (Fig. 2A). The slope of SST anomaly contours in December and January indicates poleward propagation at 105 km day^{-1}, compared to a theoretical phase speed of 100 km day^{-1} for coastal trapped internal Kelvin waves. In theory, poleward geostrophic flow induced by a Kelvin wave may transmit El Niño SST and sea-level anomalies from the equator, although Simpson shows that the 1982–1983 California anomalies were more consistent with onshore transport induced by large-scale atmospheric forcing in the north Pacific (*10*). In fact, the anomalies in the upwelling index in Fig. 2B, which indicate positive onshore transport anomalies, appear to propagate equatorward at 150 km day^{-1}. For several months beginning in April, upwelling indices returned to near or above normal and SST anomalies declined to 0.5° to 1.5°C. This moderation of El Niño is also evident in time series of sea level along the California coast (*11*) and follows a transient decline in equatorial SST anomalies that began in January and February (*12*).

The view of El Niño provided by these satellite images, especially the direct evidence of weakened coastal upwelling, could not be readily obtained from conventional ship and buoy data. One of the primary benefits of oceanographic sensors on satellites is that they provide extensive and synoptic coverage of localized mesoscale changes at the sea surface.

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8. Crosses in Fig. 1E mark surface pigment stations. Pigment algorithms are from R. C. Smith and K. A. Baker [*Mar. Biol.* **66**, 269 (1982)] for $C_{sat} < 1.5$ mg m^{-3}, and from (*7*) for $C_{sat} > 1.5$ mg m^{-3}. The C_{sat} values on 15 March 1983 matched ship values from 17 to 18 March (all < 0.5 mg m^{-3}, J. A. McGowan, Scripps Institution of Oceanography) to ±42 percent, with a bias of +23 percent. The CZCS algorithms were less successful in matching higher ship values on 19 April 1982 (up to 8 mg m^{-3}, R. W. Owen, National Marine Fisheries Service), with a root-mean-square error of ±66 percent and a bias of −35 percent. The biases reduce the apparent difference between 1982 and 1983 C_{sat} values.
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SOME EFFECTS OF EL NIÑO 1983 ON THE NORTHERN ANCHOVY

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ABSTRACT

A major California El Niño began in late 1982, bringing unusually large positive anomalies in sea-surface temperature and sea-level height. Analysis of historical records reveals a weak positive relationship between northern anchovy population growth and interannual variations in these parameters, except in the second year of major El Niño events. 1983 spawning activity was marked by an extended spawning range, dominance of small, year-old females, and faster egg maturation caused by warm water. El Niño 1983 appears to have been unfavorable for the growth of larvae, juveniles, and adults, possibly because of reduced food availability.

RESUMEN

A finales de 1982 se inició en California un fenómeno similar a El Niño, el cual originó altas anomalías positivas en las temperaturas superficiales y en el nivel del mar. El análisis de los datos históricos señala una débil relación positiva entre el incremento de la población de la anchoveta del norte, *Engraulis mordax*, y las variaciones interanuales en esos parámetros, excepto durante el segundo año de aquellos El Niño de mayor intensidad. La actividad de puesta de la anchoveta durante 1983 se caracterizó por cubrir un área más extensa, la dominancia de hembras pequeñas, de un año, y la rápida madurez de los óvulos ocasionada por la influencia de las aquas cálidas. El Niño de 1983 resultó al paracer desfavorable para el crecimiento de larvas, juveniles y adultos, debido posiblemente a una escasez de alimento.

INTRODUCTION

El Niño events have contributed to catastrophic declines in populations of seabirds and pelagic fish in the normally highly productive coastal upwelling system off Peru (Idyll 1973). An unusually strong El Niño began to affect the eastern tropical Pacific in mid-1982 (Cane 1983). Sea-surface temperature anomalies greater than +2°C were observed off California beginning in November (Auer 1982). During peak northern anchovy spawning in January-April 1983, very unusual oceanographic conditions prevailed off southern California: sea-surface temperatures were up to 3°C warmer than normal; the mixed-layer depth increased by 50 m; and unprecedented sea-level heights were recorded (Simpson 1983, Lynn 1983). This paper is a brief discussion of some consequences of El Niño for the anchovy central subpopulation between Point Conception, California, and Punta Baja, Baja California.

HISTORICAL RELATIONSHIP BETWEEN ANCHOVY AND EL NIÑO

One of the best biological time series available to relate to interannual oceanographic variability off California was recently developed by MacCall and Methot (1983, Table 3-1 therein). This 1951-82 series of annual estimates of anchovy central subpopulation spawning biomass was constructed from four separate data sets: (1) CalCOFI ichthyoplankton surveys, (2) California Department of Fish and Game acoustic surveys, (3) commercial aerial spotter logbooks, and (4) CalCOFI egg production method surveys. MacCall (MacCall and Methot 1983) fit the following population growth model to this time series:

$$B_{t+1} = aB_t^b - \delta C_t + r_t$$

where B_t is spawning biomass in year t,
C_t is total catch discounted by a factor δ,
r_t is a random error term including both measurement error and the effects of environmental anomalies,
a and b are constants.

The term δC_t represents spawners that would have survived natural mortality had they not been caught by the fishery. Parameters a and b can be related to more meaningful parameters—maximum net productivity (MNP) and the spawning biomass at which MNP occurs (BMNP)—as follows:

$$\text{MNP} = \max(aB^b - B)$$

$$\text{BMNP} = (ab)^{1/(1-b)}$$

If the model describes the *true* influence of the population on itself, then r_t would be the added effect of the environment. I solved the above equation for $ln(r_t)$, t = 1954 to 1982, using the log-transformed

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[Manuscript received January 23, 1984.]

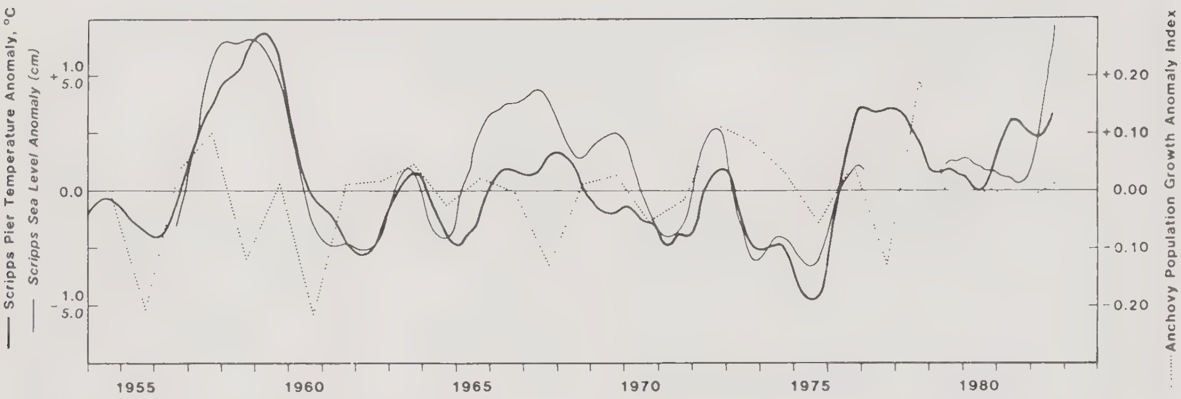

Figure 1. Time series of yearly anchovy population growth anomaly index and monthly anomalies of surface temperature and sea level at Scripps Pier.

biomass time series and MacCall's parameter values ($a=7.164$, $b=0.742$, $\delta=0.82$). The anchovy population growth anomaly index, $ln(r_t)/ln(aB_t^b)$, represents the relative deviation of annual recruitment and adult survival from what would be expected for a stock of a given size. I assume it reflects influences of interannual environmental changes, compounded by errors in the biomass estimates.

Interannual variability in the California Current is closely associated with El Niño (Chelton et al. 1982). Time series of anomalies of monthly mean surface temperature[1] and sea level[2] at Scripps Pier in La Jolla were used as indicators of environmental variability off southern California. Both series were smoothed twice by a 13-month running mean, which serves as a low-pass filter to isolate interannual variability. Coastal sea level is strongly related to seasonal and interannual variations in geostrophic flow of the California Current, with high sea levels corresponding to anomalous northward flow (Chelton et al. 1982). A linear trend of $+0.21$ cm yr^{-1} was removed from the sea-level data.

The monthly records of surface temperature and sea level are strongly correlated, although there was a notable exception to this relationship in 1981 (Figure 1). The maximum correlation ($r = +0.85$, $P << .001$) occurs when the sea-level record is lagged by one month. In comparison, Enfield and Allen (1980) found that temperature lagged sea level by 2-6 months, at interannual frequencies, in an analysis of 1950-74 records from four California shore stations. I used the smoothed Scripps Pier temperature record as an index of environmental variability associated with El Niño. Changes at La Jolla, however, may not always represent changes over the entire range of the central subpopulation.

There is no significant correlation between anomalies in anchovy population growth and surface temperature ($r = +0.04$ using December surface temperature values). However, there are large negative population growth anomalies associated with the 1957-59, 1966-68, and 1976-78 California El Niño events. The two largest anomalies, in 1955 and 1960, occur during cold or cooling years before and after the 1957-59 event. A more interesting pattern emerges when the large anomalies in 1958, 1967, and 1977 are considered: the anchovy population growth anomaly index drops well below zero in the second year of each of the three multiyear warm events observed prior to 1980.

If 1958, 1967, and 1977 are excluded from the time series, a weak positive correlation between anomalies in anchovy population growth and temperature is observed ($r = +0.32$, $0.10 > p > 0.05$). This implies that the relationship is nonlinear: i.e., relatively warm or warming years tend to be favorable for population growth, but prolonged warming is unfavorable.

SPAWNING ANOMALIES IN 1983

Spawning activity has been monitored once or twice yearly since 1980 by month-long CalCOFI egg and trawl surveys during the height of the spawning season (February-April). The 1983 spawning range, indicated by the distribution of first-day eggs, extended beyond Point Conception at the northwest edge of the Southern California Bight (Figure 2). In contrast, spawning during 1980-82 was apparently excluded from this region by a plume of cold California Current water to the south of Point Conception (Lasker et al. 1981; Fiedler 1983). The February 21, 1981, satellite image

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[1] E. Stewart, Scripps Institution of Oceanography

[2] D. Brown, Scripps Institution of Oceanography

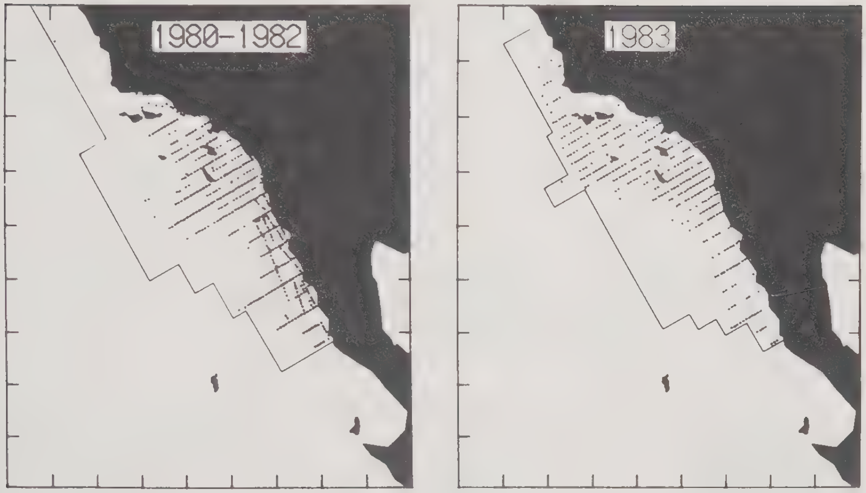

Figure 2. Distribution of CalVET tows with first-day eggs on CalCOFI cruises: *left*, 8003, 8102, and 8202; *right*, 8302. Boundaries mark limit of sampling effort.

in Figure 3a shows the influence of this cold-water boundary (the six lines of stations south of Point Conception were occupied on February 15-20). The boundary corresponded approximately to the 14°C isotherm.

Sea-surface temperatures (SSTs) off southern California were 1°-3°C warmer than the 1942-69 means during the first few months of 1983 (Auer 1983). Figure 3b illustrates the unusual SST pattern present in the Southern California Bight during CalCOFI cruise 8302: there was no cold-water plume south of Point Conception. In fact, the 14°C isotherm remained north of Morro Bay at lat. 35°20′N from February until the middle of March, when it moved south to Point Conception[3]. No SSTs colder than 14°C were measured on this cruise, although the warmest temperatures did not exceed the extreme of 17.7°C recorded on cruise 8003

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[3] Weekly GOSSTCOMP sea-surface temperature maps distributed by NOAA, National Environmental Satellite Data and Information Service, Washington, D.C.

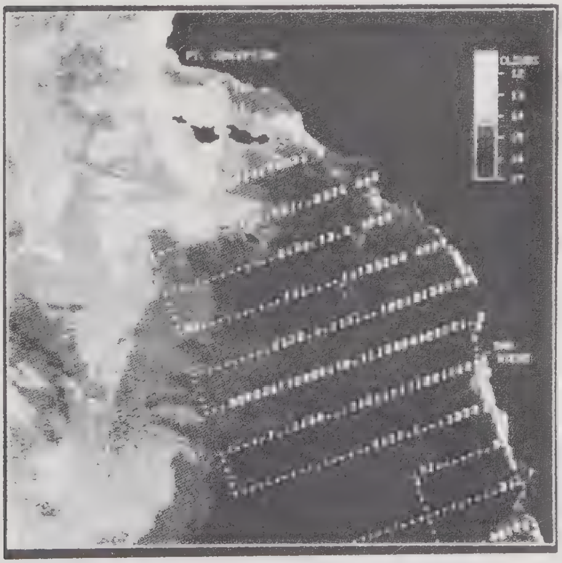

Figure 3a. CalCOFI 8102 A-day anchovy egg distribution, February 12-March 10, 1981. · = 0, 1 = 1 – 4, 2 = 5 – 15, 3 = 16 – 157 eggs/0.05 m². Sea-surface temperature from NOAA-6 AVHRR, channel 4, February 21, 1981

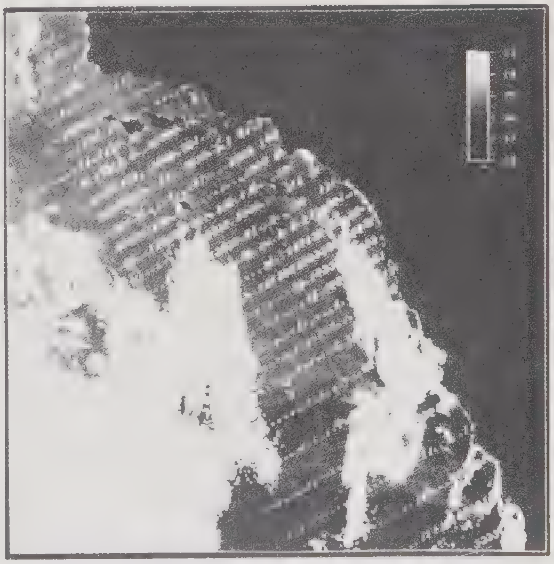

Figure 3b. CalCOFI 8302 A-day anchovy egg distribution, February 9-March 29, 1983. · = 0, 1 = 1 – 3, 2 = 4 – 12, 3 = 13 – 229 eggs/0.05 m². Sea-surface temperature from NOAA-7 AVHRR, channels 4 and 5, March 15, 1983.

TABLE 1
Egg Production Estimates of Anchovy Spawning Parameters

	1980[a]	1981[a]	1982[a]	1983[b]
Spawning biomass (x10^3 metric tons)	870	635	415	625
Average female weight (g)	17.4	13.4	18.8	11.2
Sex ratio by weight (females/total)	0.48	0.50	0.47	0.55
Spawning frequency of mature females (1/day)	0.14	0.11	0.12	0.09
Batch fecundity (eggs/batch)	7750	8330	10840	5300
Population production of spawned eggs (x10^{12} eggs/day)	26.3	21.0	13.5	17.2
Incubation period (days)	2.71	2.75	2.91	2.56
Egg mortality rate (1/day)	0.45	0.14	0.16	0.18
Population production of hatching eggs (x10^{12} eggs/day)	7.7	14.3	8.5	10.8

[a] Picquelle and Hewitt (1983). Original estimates of egg production and spawning biomass were elevated by a factor of 1/0.91 to correct for 91% retention of eggs by nets on 1980-82 surveys (R. Hewitt, NMFS/Southwest Fisheries Center, pers. comm.).
[b] Picquelle and Hewitt (1984).

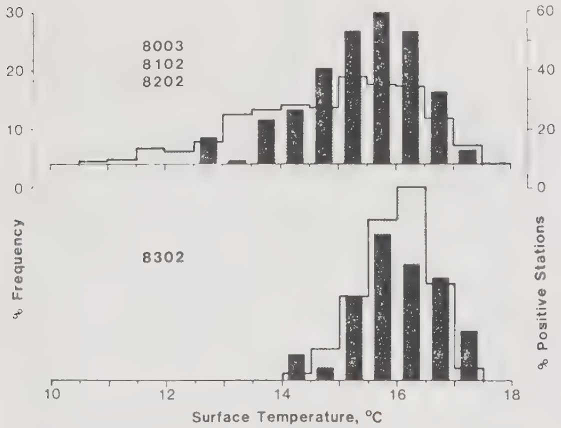

Figure 4. Frequency distributions of CalCOFI stations by surface temperature (stippled), with frequency of positive A-day anchovy egg catches within each temperature interval (solid bars), for 1980-82 (3 cruises, 2036 stations) and 1983 (850 stations).

(Figure 4). Spawning success, measured by frequency of positive egg stations in a temperature interval, was shifted slightly to warmer temperatures in 1983. Several factors associated with El Niño contributed to changes in the SST field off southern California at this time: diminished wind-driven flow of the California Current (Simpson 1983), an anomalously strong poleward countercurrent (Lynn 1983), and weakened coastal upwelling. Monthly upwelling indices between lat. 30° and 36°N averaged 70% (range 8%-309%) below the 1948-69 means during January-April 1983.[4]

Several 1983 spawning parameters appear to have been anomalous (Table 1), although the limited history of egg production surveys, beginning in 1980, precludes statistical evaluation of departures from "normal." Estimated spawning biomass increased for the first time since 1979. However, females were young and of low body weight, resulting in subnormal spawning frequency and fecundity. A slightly increased egg maturation rate, probably related to warmer water temperatures, was not sufficient to reduce egg mortality to less than normal. El Niño seems to have had no net effect on the total production of hatching eggs in 1983.

GROWTH AND SURVIVAL DURING EL NIÑO

Three environmental processes have received much attention as potential regulators of recruitment of pelagic fish and, in particular, northern anchovy. Fluctuations in primary productivity associated with upwelling are important in the California Current as in other major upwelling regions (Bakun and Parrish 1980). Availability of appropriate food organisms in dense, subsurface layers is critical for survival of first-feeding anchovy larvae (Lasker 1978). Finally, offshore transport of larvae by wind-induced Ekman flow may be especially important where seasonally strong flow occurs over a narrow continental shelf, as in central and northern California (Parrish et al. 1981). We know less about factors affecting the survival of juvenile anchovy, after metamorphosis at the age of ~50 days, but it is likely that food availability continues to be important. Unusual conditions off southern California during the first few months of 1983 may have affected food availability:

1. Coastal upwelling was weak from January through April.
2. The thermocline was up to 50 m deeper than the long-term mean (Simpson 1983). The chlorophyll maximum layer, which often indicates a subsurface accumulation of phytoplankton, was also 10 to 50 m deeper than normal (McGowan 1983).
3. Phytoplankton pigment levels estimated from satellite data were relatively low in March (Fiedler,

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[4] Monthly analyses of North Pacific wind-driven surface transport, from surface marine weather observations, distributed by NMFS/Pacific Environmental Group, Monterey, California 93942. See also Bakun (1973).

1984). Vertically integrated chlorophyll concentrations along CalCOFI line 90 steadily declined from March to August, when they were about one-quarter the normal value. (J. A. McGowan, Scripps Institution of Oceanography, pers. comm.).

4. The coast was hit by violent storms in late January and in late February and early March because of an equatorward shift of the normal storm track.

This evidence, although indirect, indicates reduced phytoplankton productivity in the spawning habitat of the northern anchovy. Turbulent mixing by the winter storms could have dispersed any near-surface layers of phytoplankton that would normally support first-feeding larvae.

The California Department of Fish and Game has conducted trawl surveys of pelagic fish off California and Baja California since 1966. Preliminary data are available from two surveys in late 1983: September 23-October 12 from Blanca Bay (lat. 28°50′N) to Point Conception; and November 2-21 in the Southern California Bight[5]. The catch rate for 1983 year-class anchovy was not unusual: among eight annual surveys since 1976, the 1983 rate ranked fourth by weight and third by number of fish. However, these fish were remarkably small, with a mode of 65-75 mm, compared to 85-95 mm for young-of-the-year in 1976-82.

Adult fish were also abnormally small, with a mode of 100-105 mm, compared to an expected 115-120 mm. Yet these fish were still much larger than southern subpopulation fish (south of lat. 29°N), which averaged 87 mm in 1966-73, with only 10% exceeding 106 mm (Mais 1974). The small size of central subpopulation anchovy in 1983 cannot be explained simply by transport or migration of smaller southern subpopulation fish: very few or no anchovies were caught south of Punta Baja (lat. 30°N) on the trawl surveys. The anomaly more likely reflects reduced growth during El Niño 1983. The 1982 year-class fish appeared to have grown by only 10 mm since a survey in February 1983, compared to a normal growth increment of 15 mm for year-old fish from February to November (Mallicoate and Parrish 1981).

CONCLUSIONS

Anchovy population growth since 1954 has shown a weak positive correlation with interannual sea-surface temperature variations. This relationship has broken down, however, in the second year of major California El Niño events in 1957-59, 1966-68, and 1976-78. The 1983 California El Niño brought large and, in some cases, unprecedented oceanographic anomalies beginning just before the peak northern anchovy spawning season. Several aspects of 1983 spawning were unusual: an extended spawning range, relatively young and small-sized spawners, and rapid egg maturation. The resultant production of hatching eggs was not unusually large or small, and no marked effect on the size of the 1983 year class could be detected by the end of the year. However, both juveniles and adults appeared to be abnormally small, possibly because of reduced food availability throughout the year.

As 1983 ended, the consensus of meteorologists and oceanographers was that El Niño was well into its final, decay phase at the equator (Rasmusson and Wallace 1983; Cane 1983). However, the California El Niño lingered: sea-surface temperature anomalies > 1°C and subsurface anomalies > 2°C were observed up to 400 km offshore between Point Reyes and Santa Monica on CalCOFI cruise 8401 (R. Lynn, NMFS/Southwest Fisheries Center, pers. comm.; see also Auer 1984). The ultimate effect of the 1983 California El Niño may yet be manifested in the size of the 1984 year class of northern anchovy.

ACKNOWLEDGMENTS

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Fisheries Applications of Satellite Data in the Eastern North Pacific

PAUL C. FIEDLER, GARY B. SMITH, and R. MICHAEL LAURS

ABSTRACT—Satellite sensors provide extensive and detailed images of sea surface temperature and color. Synoptic daily sampling by satellites gives a unique view of the ocean surface that can be extremely useful when used in conjunction with conventional shipboard data. Current and potential applications of satellite data off the U.S. Pacific coast and Alaska include interpretation of ship survey data, explanation of pelagic fisheries distributions, prediction of stock recruitment, spatial/temporal monitoring of the coastal zone and sea ice, studies of migration routes and timing, and production of charts to aid commercial fisheries.

Introduction

Remote sensing of the ocean is playing an increasingly important role in fishery research and fish harvesting along the Pacific coast of the United States and Canada. Satellite sensors make synoptic measurements of water temperature and color, winds, ice cover, wave height, and surface currents over large areas of the ocean surface. Variations in these ocean conditions play key roles in natural fluctuations of fish stocks and in their vulnerability to harvesting.

The promise of remote sensing techniques for fisheries research, management, and exploitation has been recognized since the early 1960's when the first visible and infrared images of the earth's surface were obtained from orbit. However, successful applications have only recently been realized with the advent of advanced and sensitive radiometers, high-speed data processing, and the availability of imagery to fishery scientists and fishermen.

Gower (1982) provides a useful overview of the different kinds of remote sensing data relevant to fisheries science and oceanography. Laurs and Brucks (In press) review living marine resources applications in the United States. Yamanaka (1982) gives examples of some uses of satellite data for fisheries applications off Japan. Other potential, ocean-related uses of remote sensing data were discussed by Montgomery (1981). This paper will review the satellite sensors currently measuring sea surface temperature and ocean color, data processing and availability, and several examples of recent and potential applications to eastern North Pacific fisheries.

Satellites provide a unique view of the ocean by covering large areas synoptically. Coverage of historically data-poor areas is particularly useful. However, satellite measurements are usually limited to the surface or near-surface layers in cloud-free areas. Therefore, satellite data complement conventional shipboard observations but cannot replace them. The best research approach often requires close coordination of the two sources of information. In this way, the evolving capabilities of satellite remote sensing are providing a powerful tool to enhance the efficient use of living marine resources.

Satellite Sensors

A variety of instruments measure radiance from the earth's surface in visible, thermal infrared (IR), and microwave wavelength bands (Table 1). The most readily available and useful data come from the Advanced Very High Resolution Radiometer (AVHRR) on meteorological satellites operated by the National Oceanic and Atmospheric Administration (NOAA) and the Coastal Zone Color Scanner (CZCS) on the experimental Nimbus-7 satellite operated by the National Aeronautics and Space Administration (NASA). These advanced sensors are characterized by high sensitivity in narrow wavelength bands, fine ground resolution, and extensive data archival.

Satellites receive electromagnetic radiation emitted from the sea surface (the IR temperature signal) and back scattered from below the surface (the visible ocean color signal). These signals are contaminated by reflection from the sea surface and clouds, and by absorption, emission, and scatter by atmospheric particulates and molecules. Some of these errors can be eliminated or minimized very simply. For example, sunglint and "limb darkening" (by long atmosphere paths at oblique viewing angles) are avoided by constraining the viewing geometry of the sensor. Corrections of some other errors, however, require advanced image processing methods.

Dense clouds may so completely absorb visible and IR radiation from the sea surface that no type of data

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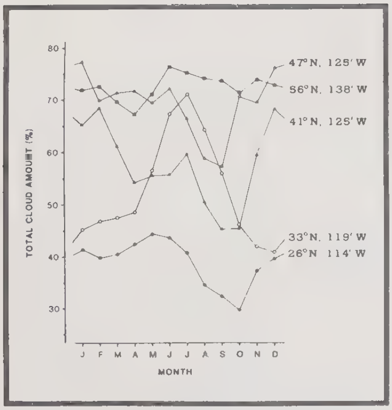

Figure 1.—Mean monthly total cloud amount over coastal waters, from surface marine weather observations, 1921-72 (Nelson and Husby, 1983): Baja California (27°N, 115°W), Southern California Bight (33°N, 119°W), Cape Mendocino (41°N, 125°W), Vancouver Island (48°N, 126°W). Gulf of Alaska data (56°N, 138°W) are from satellite observations, 1967-72 (Sadler et al., 1976), intercalibrated against data from Nelson and Husby (1983).

Table 1.—Some satellite sensors measuring visible, infrared, or microwave radiance for oceanographic measurements. Wavelengths are band midpoints. Ground resolution dimensions are directly beneath the satellite.

Sensor[1]	Satellite	Channel	Spectral band	Wavelength (μm)	Scan width (km)	Ground resolution (km)	Primary measurements
AVHRR	TIROS-N	1	Visible	0.63	3,000	1.1	Sea surface temperature, sea ice
	NOAA-6, 7, 8	2	Near-infrared	0.91			
		3	Infrared	3.74			
		4	Infrared	10.8			
		[2]5	Infrared	[2]12.0			
CZCS	Nimbus-7	1	Visible	0.44	1,566	0.825	Phytoplankton pigments, turbidity, sea surface temperature
		2	Visible	0.52			
		3	Visible	0.55			
		4	Visible	0.67			
		5	Near-infrared	0.75			
		6	Infrared	11.5			
MSS	LANDSAT	1	Visible	0.55	185	0.079	Water color, turbidity, sea ice
		2	Visible	0.65			
		3	Near-infrared	0.75			
		4	Near-infrared	0.95			
VISSR	GOES	1	Visible	0.62	Earth disk	7×3	Cloud cover, sea surface temperature
		2	Infrared	11.5			
SMMR	Nimbus-7	1	Microwave	4.54×10^4	600	20-100	Sea surface temperature, sea ice, near-surface winds
	SEASAT	2	Microwave	2.8×10^4			
		3	Microwave	1.66×10^4			
		4	Microwave	1.36×10^4			
		5	Microwave	0.81×10^4			

[1]Sensors: AVHRR = Advanced Very High Resolution Radiometer; CZCS = Coastal Zone Color Scanner; MSS = Multispectral Scanner; VISSR = Visible and Infrared Spin Scan Radiometer; SMMR = Scanning Multichannel Microwave Radiometer.

[2]Channel 5 on NOAA-7 and NOAA-8 satellites only.

processing can retrieve a useful signal. Clouds severely limit satellite coverage of the sea surface in some regions of the eastern North Pacific, particularly north of lat. 40°N (Fig. 1). South of lat. 27°N, off Baja California, mean monthly cloud cover is consistently less than 50 percent, due to persistent offshore flow of dry continental air. From lat. 30°N to 38°N, coastal waters are covered by a dense layer of low stratus clouds during the summer upwelling season (Nelson and Husby, 1983). The most favorable conditions for remote sensing at these latitudes are found from October through March or April, especially during occasional brief periods when Santa Ana winds blow warm, dry desert air offshore and produce cloud-free conditions up to 1,000 km from the coast.

In contrast, the most cloud-free conditions at lat. 40°-50°N are found in late summer, from August to October. Mean monthly cloud cover increases to the north and is consistently 70 percent or greater in the Gulf of Alaska, although March and April may be relatively clear. As a general rule, percent cloud cover increases by at least 10 percent from the coast to a distance on the order of 200 km offshore in the eastern North Pacific (Nelson and Husby, 1983).

The probability of cloud-free conditions in a region of interest during regular satellite passes is loosely reflected in these monthly cloud cover statistics. Cloud cover restricts the extent to which satellite data can be anticipated, or depended upon, to be available. Whereas it may be possible to obtain regular daily or weekly coverage of sea surface features in the south, such as in the Southern California Bight, in the north there are generally more frequent and longer data gaps. Satellite coverage of ocean features in the Alaska region is characteristically limited to occasional cloud-free scenes that, despite being infrequent, can be rich in information. Microwave radiometers can measure sea surface temperature through clouds, but with a lower sensitivity and much coarser resolution than IR radiometers.

Data Processing

The AVHRR measures thermal infrared radiant energy in three wavelength bands (Table 1). Temperature calibration data are obtained by scanning deep space and internal blackbody targets. Accurate sea surface temperatures are calculated from empirical regressions of ship and buoy temperatures on satellite temperatures in two or three bands. Such multispectral corrections are based on the different response of each band to the cold bias caused by atmospheric water vapor (McClain et al., 1983). Pixels (samples) containing clouds even smaller than the sensor's field of view are screened in daytime passes using the near-infrared albedo data from channel 2 (Bernstein, 1982).

The CZCS measures visible light in five narrow wavelength bands selected for estimating phytoplankton pigments, suspended sediments, and dissolved organic matter. Up to 90 percent of the visible radiance received at the satellite is skylight reflected and scattered within the atmosphere. Corrections are based on assumptions that the red light emitted by the ocean and measured by channel 4 is either negligible or can be accurately predicted from radiances in other bands. The atmospheric radiance measured by channel 4 can then be related to atmospheric radiances in other channels using known spectral properties of atmospheric scattering (Gordon et al., 1983). Corrected ratios of blue to yellow-green (channel 1/channel 3) or green to yellow-green (channel 2/channel 3) radiance are then used to calculate phytoplankton pigment concentration from empirical regression relationships (Smith and Baker, 1982).

Satellite data, properly corrected for the various errors described above, have been validated by sea truth data from ships to ± <1°C (Bernstein, 1982) and ±0.4 log chlorophyll concentration (Smith and Baker, 1982). While important subsurface features such as chlorophyll maximum layers and some cold-core eddies or oceanic fronts may not be detected by satellites, the measured parameters are, in general, closely related to properties such as mixed-layer temperature and integrated chlorophyll or primary productivity in the euphotic zone (Smith, 1981).

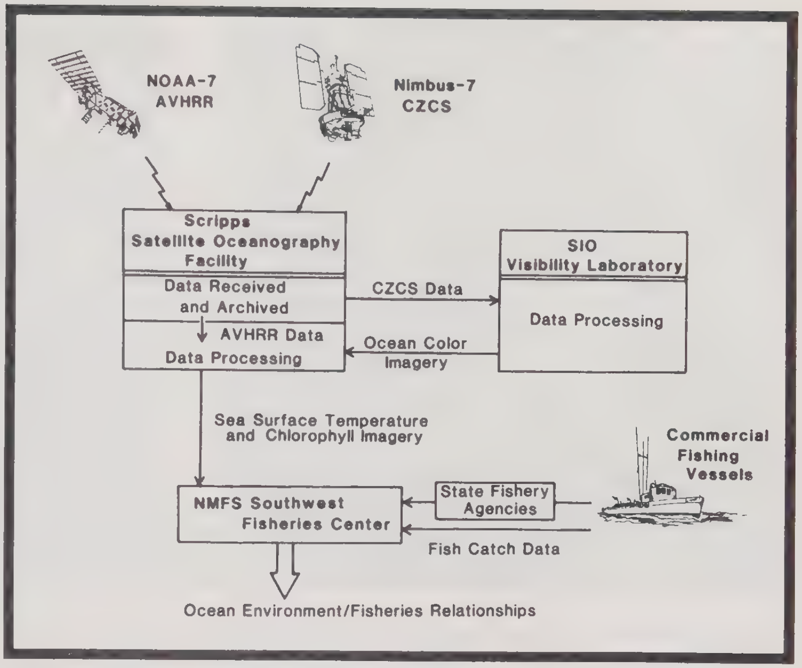

Figure 2.—Satellite data collection and processing network utilized by the National Marine Fisheries Service on the west coast.

Data Availability

Applications of satellite data are ultimately limited by their availability. Ideally, a user would have immediate access to data received directly from satellites and conveniently archived, with data processing facilities at his fingertips. This ideal has been approached by an arrangement at the Satellite Oceanography Facility of Scripps Institution of Oceanography in La Jolla, Calif., for most of the work reported here (Fig. 2). Similar arrangements, lacking direct data reception capabilities, have been established at the University of Miami and by the Northeast Area Remote Sensing System, which is a regional association of university, industry, and government organizations that was recently formed in the northeastern United States.

Global satellite data are archived by the Satellite Data Services Division of NOAA and are available to the public, although acquisition may require several months and a large backlog of CZCS data is unprocessed. AVHRR and CZCS data are available in various forms including photographic prints and negatives, digital data on magnetic tapes, and maps of derived sea surface temperature and ice cover. These products and a catalog of available CZCS data are available from the National Environmental Satellite Data and Information Service, Satellite Data Services Division, NOAA, Room 100, World Weather Building, Washington, DC 20233. Detailed procedures for obtaining environmental satellite data are given in Cornillon[1]. In general, photographic copies of raw data are of limited value and a user must have access to a computer-based, image processing system to extract useful information from satellite data on digital tapes (this situation may change in the future if products derived from satellite data are offered by commercial processing enterprises).

Applications

We briefly review here examples of general applications of satellite data to fisheries research and management problems along the Pacific coast between California and Alaska. Some of these examples have been published elsewhere, but none of the applications has as yet been fully realized.

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[1] Cornillon, P. 1982. A guide to environmental satellite data. Univ. R. I. Mar. Tech. Rep. 79, 469 p. Available for $20.00 from the University of Rhode Island, Marine Advisory Service, Publication Unit, Narragansett, RI 02882.

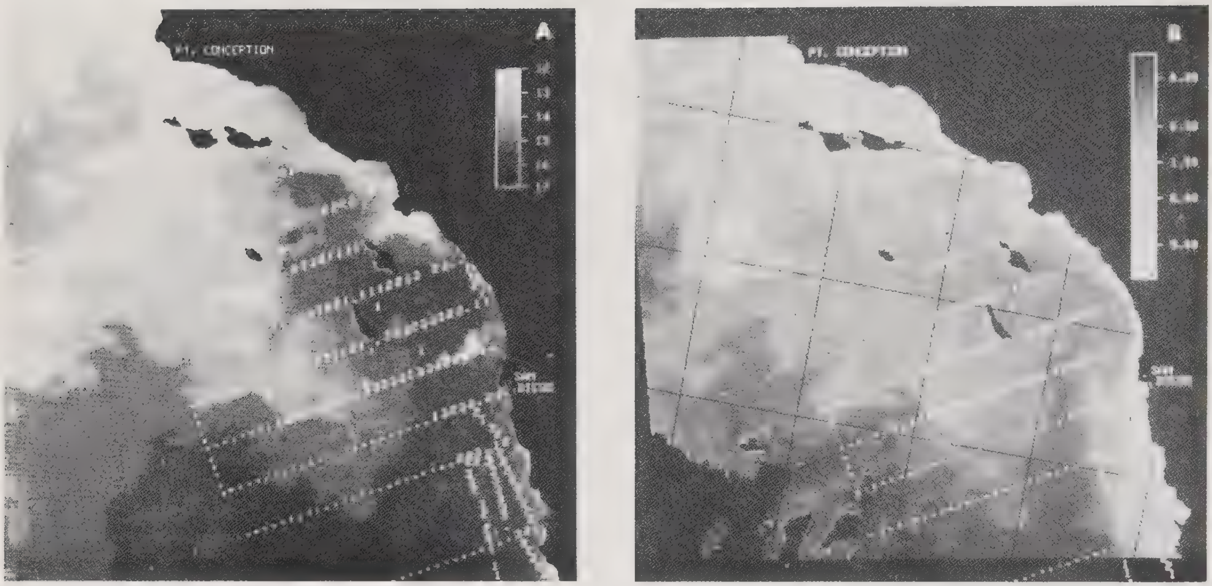

Figure 3.—Northern anchovy egg distribution, 20 March-10 April 1980; • = 0, 1 = 1-4, 2 = 5-17, 3 = 18-245 eggs/0.05 m^2. Top photo (A) is sea surface temperature (°C) from NOAA-6 AVHRR, 7 April 1980; Photo B is of phytoplankton pigments (mg m^{-3}) from Nimbus-7 CZCS, 8 April 1980.

Interpretation of Ship Survey Data

A large stock of northern anchovy, *Engraulis mordax,* is found off southern California, where intensive egg surveys have been conducted since 1980 to estimate spawning biomass. Satellite images of sea surface temperature and phytoplankton pigment concentration, obtained during an egg survey in April 1980, depict environmental limits on the range of spawning anchovy (Fig. 3). North of San Diego, no eggs were found in water colder than 14°C. To the south, spawning northern anchovy were confined along the coast to a narrow band of water with high pigment concentrations. Similar distribution patterns were observed in 1981 and 1982 (Lasker et al., 1981; Fiedler, 1983).

The distribution of spawning adults may reflect the critical need by first-feeding larvae for aggregations of suitable food organisms in a stable water column. The environmental limits revealed by the satellite images would not have been revealed by the egg survey data alone, because phytoplankton pigments were not measured and spatial coverage was limited.

Satellites data may be used to interpret the large-scale patterns and possible causes of spatial/temporal variability in other types of ship survey data. Most measurements of fish eggs and larvae, plankton concentrations, chlorophyll, nutrients, temperature, and salinity are made at point locations at regular intervals along transects or in grid patterns. Remote sensing data collected concurrently, if available, may provide valuable information on factors contributing to patterns in the shipboard data and on conditions beyond the area surveyed. Besides the insight that usually results from a synoptic view, this information is important in evaluating the validity of interpolation and extrapolation of ship survey results.

Pelagic Fisheries Distribution

Albacore, *Thunnus alalunga*, is a migratory oceanic tuna that is an important target species for jigfishing, live bait, and recreational fishing along the U.S. Pacific coast from July to October. Fishermen search for aggregations of these fish in warm, blue oceanic waters near temperature or water color fronts at the offshore edge of productive coastal waters. Daily catch records during peak fishing in late summer 1981 were taken from logbooks submitted to west coast state fisheries agencies. Concentrations of fishing activity and large catches indicate sites of albacore aggregations.

Satellite images of sea surface temperature and phytoplankton pigment concentrations clearly show favorable sites for aggregations in pockets of warm, blue oceanic water intruding into the colder and more turbid coastal water mass (Fig. 4; Laurs et al., In press). Albacore are visual predators and may feed most efficiently in the clear water adjacent to coastal waters where prey densities are higher. Albacore fishermen, running several days out of port in small boats to reach offshore fishing grounds, can benefit from timely maps of sea surface temperature and ocean color gradients derived from satellite data. Potential benefits include decreased search time, lower fuel use, and increased catches.

Satellite data may be applied to

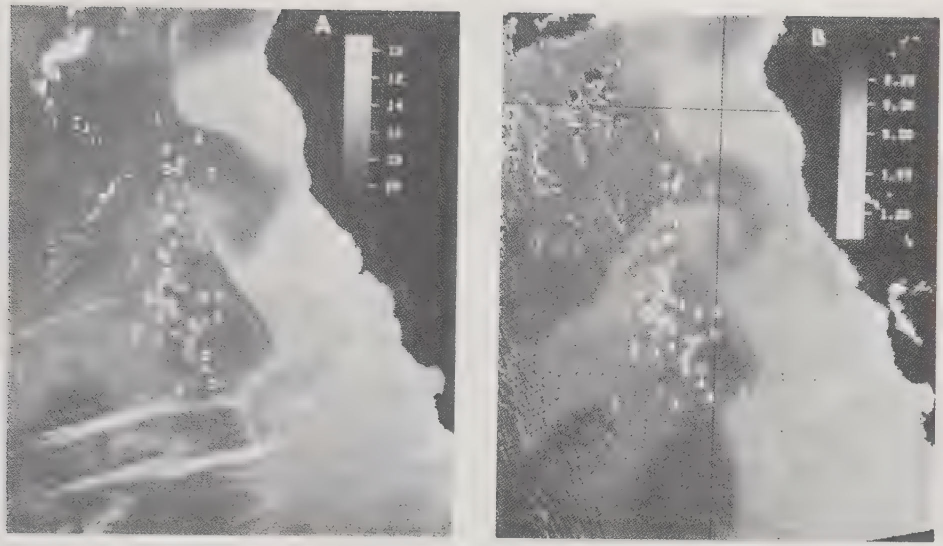

Figure 4.—Daily albacore catches off central California, 19-24 September 1981: 1 = 0-27, 2 = 33-63, 3 = 64-81, 4 = 87-140, 5 = 148-750 fish/boat. A is sea surface temperature (°C) from NOAA-7 AVHRR, 21 September 1981; B is phytoplankton pigments (mg m^{-3}) from Nimbus-7 CZCS, 22 September 1981.

other pelagic fisheries, both to direct fishing effort and for fisheries management. In the Pacific Northwest and off Alaska, five species of Pacific salmon—sockeye salmon, *Oncorhynchus nerka*; chum salmon, *O. keta;* pink salmon, *O. gorbuscha*; chinook salmon, *O. tshawytscha*; and coho salmon, *O. kisutch*—are important resources for a large fishing industry. During their oceanic life history phase, these salmon are caught by power or hand-trolling boats using methods similar to albacore fishing. The study described by Borstad et al. (1982) is an example of a use of remote sensing techniques to study relationships between salmon distributions, fishing, and oceanographic conditions. Other pelagic resources for which there may be analogous applications include Pacific herring, *Clupea harengus pallasi,* off Alaska; jack mackerel, *Trachurus symmetricus,* and Pacific mackerel, *Scomber japonicus,* off California; and bluefin tuna, *Thunnus thynnus orientalis,* off Baja California.

Stock Recruitment Predictions

An application of satellite data that merits investigation is the improved understanding and prediction of variations in recruitment to coastal fish stocks. In the eastern North Pacific, offshore transport and turbulent mixing may have important effects on the larval survival and subsequent recruitment of some species (Bakun and Parrish, 1982). Both processes are driven by surface wind stress. Offshore transport removes eggs and larvae from productive nearshore nursery grounds. This may be most important where strong seasonal upwelling occurs over a narrow continental shelf, as it does along the U.S. coast north of lat. 34°N. Turbulent mixing reduces stratification of the near-surface water column and disrupts aggregations of food organisms required for successful first feeding by newly hatched larvae (Lasker, 1981).

Variations in annual recruitment of Pacific whiting, *Merluccius productus,* have been related to monthly mean Ekman transport estimated from equatorward wind stress off central California (Bailey, 1981). Fiedler (1984) has used AVHRR imagery to document interannual changes in the sea surface temperature field related to variations in coastal upwelling off the U.S. Pacific coast. Satellite imagery has also revealed that offshore transport is a highly irregular process in both time and space, manifested as meandering jets and eddies of cold water (e.g. Fig. 5). Offshore transport could perhaps be quantified by measuring the areal extent of relatively cold water nearshore or the offshore displacement of frontal features between daily satellite passes. This application may be extended to other species for which there is evidence of similar environmental effects (e.g. Hayman and Tyler, 1980; Bakun and Parrish, 1982).

The seasonal timing and spatial location of northern anchovy spawning has been related to turbulent mixing, as indexed by the cube of mean surface wind speed in historical marine weather observations, by Husby and Nelson (1982). They suggested that strong year classes may depend upon the occurrence of "time-space windows" with sufficiently low turbulence to allow development of layers of food organisms.

The magnitude and direction of surface wind stress are directly

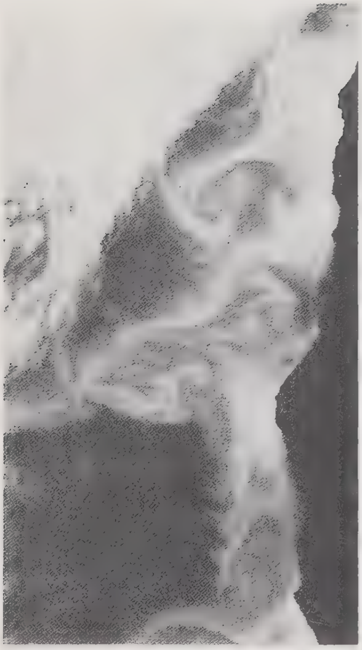

Figure 5.—Localized offshore transport of cold upwelled water (whiter shades) off northern California and southern Oregon. The three major coastal landforms, from top to bottom, are Cape Blanco, Cape Mendocino, and Point Arena. White features in the top left corner are clouds. Image from NOAA-7 AVHRR channel 4, 14 June 1982.

measurable by microwave sensors such as the scatterometer which flew on the short-lived SEASAT satellite in 1978. The U.S. government has not yet committed funds to orbit another such sensor, for which there are many potential scientific and commercial applications (NASA Satellite Wind Stress Working Group, 1982). Fisheries applications might include the real-time planning of fishing operations to avoid adverse sea state conditions, as well as the measurement of surface winds driving environmental processes affecting recruitment into coastal fish stocks. These benefits would be particularly significant in northern areas, such as the Pacific Northwest and Alaska regions, where present remote sensing coverage by visible and infrared sensors is usually limited by cloud cover.

Coastal Zone Monitoring

Mesoscale processes, such as upwelling and eddy formation, are very important components of the spatial and temporal variability of eastern North Pacific coastal waters, especially in the complex California Current System. Extensive and high-resolution satellite data are particularly valuable for studies of these processes (Bernstein et al., 1977). Anomalous ocean conditions along the U.S. Pacific coast were monitored during the 1982-83 El Niño event using AVHRR and CZCS data (Fiedler, 1984). Localized sea surface temperature anomalies up to +6°C were observed. Reduced coastal upwelling during the first half of the year was detected in patterns of cold, nearshore surface waters. CZCS images of the Southern California Bight indicated reduced phytoplankton productivity. This event affected many commercial and sport fisheries along the coast (Anonymous, 1984).

Monitoring coastal zone variability within a year or season with satellite data may be useful for developing better release strategies for hatchery-reared juvenile salmonids by enabling management decisions to be more adaptive and based on conditions in nearshore nursery areas. It might be possible to improve the growth and survival of hatchery-reared salmon by scheduling releases during periods of most favorable ocean conditions. AVHRR and CZCS imagery could be used as sources of information on sea surface temperature, river plume trajectory, upwelling intensity, primary production, and the oceanic frontal areas associated with each of these factors. Small improvements in the survival of juveniles released from hatcheries could result in substantial increases in the numbers of returning adults. If successful, this application would be particularly important in the Pacific Northwest and Alaska region, where hatchery operations are extensive and salmon resources have high value.

Salmon enhancement programs on the Columbia River, the largest river on the Pacific Coast of North America, provide an example of the potential. The National Marine Fisheries Service funds 22 salmon hatcheries and 7 rearing ponds on the Columbia River at an annual cost exceeding $4.5 million. Each year, these facilities culture and release 80-100 million salmon smolts in late April and early May. The present release schedule is decided largely on the basis of administrative criteria, tradition, and attempts to emulate nature. However, survival rates for these hatchery-reared salmon are relatively low, only about 3.7 percent (range, 0.23 to 12.35 percent) for coho salmon in their first year (Mathews, 1980).

There is increasing evidence that juvenile salmon survival, and subsequent adult returns, are critically influenced by conditions in the ocean environment within the first 6 months after hatchery release (Hartt, 1980; Wahle and Zaugg, 1982). Important factors may be food availability and the extent that food limitations occur in the nursery habitats as a result of crowding. On the Columbia River, although hatchery-reared salmon pass downstream and through the lower river and estuary relatively rapidly, significant losses occur in each of these migratory stages and areas. After reaching the ocean, juvenile salmon typically migrate along a relatively narrow coastal belt (Hartt, 1980). In purse seine studies off the Columbia River, juvenile salmonids (<50 cm) have been found to be distributed mainly within 28 km of shore; chinook salmon and steelhead, *Salmo gairdneri,* were distributed almost entirely in the river plume (Miller et al., 1983). Upwelling and its effects on food production have been related to juvenile survival and adult salmon production (Gunsolus[2]). A better understanding of these environmental relationships is a goal of current research.

Figure 6 shows three satellite images of sea surface temperatures along the Pacific Northwest coast during summer 1982, illustrating changes in coastal conditions that can occur over relatively short (2-3 week) time intervals. On 5 July, coastal upwelling was very weak, although signs of intensification were developing at Cape Mendocino. By 23 July, upwelling had intensified considerably, especially to the north. By 18 August, however, upwelling was again weaker. Changes in the mesoscale pattern of cold-water jets and meanders can be seen. In the latter two images, the Columbia River plume is indicated by a dark, warm-water break in the band of cold, upwelled water along the coast.

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[2] Gunsolus, R. T. 1978. The status of Oregon coho and recommendations for managing the production, harvest, and escapement of wild and hatchery-reared stocks. Oreg. Dep. Fish Wildl., Columbia Reg. Off., 17330 S.E. Evelyn St., Clackamas, OR 97015. Unpubl. manuscr., 59 p.

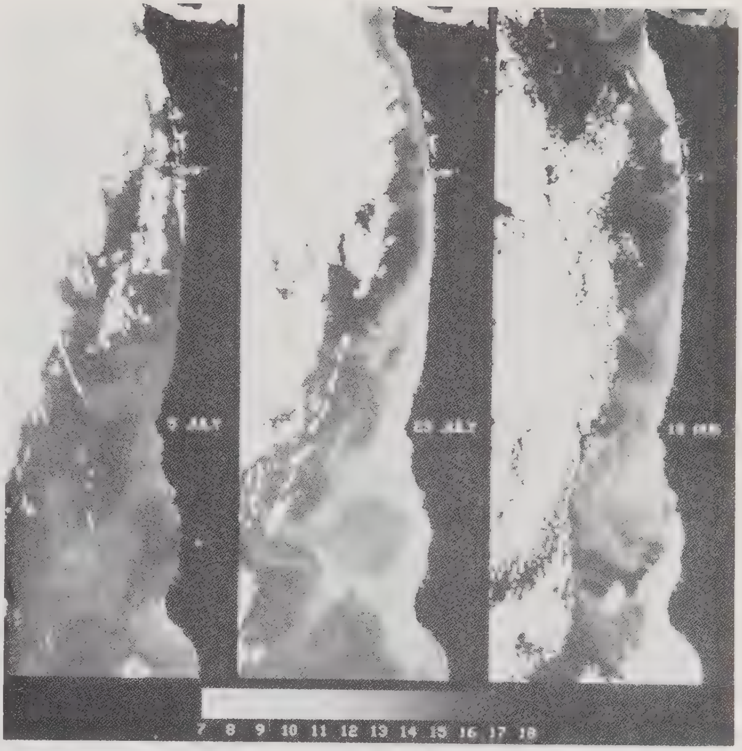

Figure 6.—Variations in the intensity and pattern of coastal upwelling off the Pacific Northwest between lat. 39°00′N and 48°30′N, July-August 1982. Sea surface temperature (°C) from NOAA-7 AVHRR channels 4 and 5. Clouds (white) screened with channel 2 data.

Monitoring Sea Ice

Sea ice is an important seasonal feature of the Alaskan environment that can be monitored by satellite coverage (Weeks, 1981; McNutt, 1981). Ice affects commercial fishing activities by threatening vessel safety, limiting navigation and access, and damaging fishing gear. Yet sometimes waters near the edge of pack ice can offer shelter or rich fishing grounds. Ice is also important because of its significance in the ecology of, and as a habitat for, northern marine mammals.

In the eastern North Pacific, winter ice cover occurs in inlets along the coasts of southeastern Alaska, the Gulf of Alaska, and the Aleutian Islands. Its formation is often associated with freshwater runoff, such as in Cook Inlet (Poole and Hufford, 1982). Freshwater ice forms on stream and river deltas, then sea ice forms in lower parts of the embayments. However, much greater ice cover occurs in the extended area to the north. Ice covers the Chukchi Sea, Bering Strait, and nearly the entire northeast half of the eastern Bering Sea during winter and spring. Movements of pack ice in the Bering Sea are influenced by winds and water currents, and are highly dynamic.

Ice off the North Slope, along the southern coast of Alaska, and in the Bering Sea, is monitored routinely by the National Weather Service. When cloud cover permits, ice and open water can be discriminated with a 1 km resolution using AVHRR visible and infrared data (Fig. 7). Combined with data from the Nimbus-7 Scanning Multichannel Microwave Radiometer, which are not influenced by clouds but have a resolution of 60 km, large-scale maps of ice coverage or concentration are produced. Some information about ice type (age and thickness) can be gleaned from satellite data, but the analysis is supplemented by aerial reconnaissance and reports from ships and shore stations. Ice analysis maps are distributed to users in the fishing and oil industries three times a week by radio facsimile and once a week by mail.

Winter fisheries affected by ice cover in the eastern Bering Sea include: Foreign groundfish fisheries, involving 200-300 vessels per year and an annual catch of about 1.3 million metric tons (Bakkala et al., 1979); highly-valued U.S. fisheries for king crab, *Paralithodes* spp., and snow (Tanner) crab, *Chionoecetes* spp. (Otto, 1981); and U.S. fisheries for Pacific herring that take place along the north shore of Bristol Bay. Vessels operating in these fisheries often need to work around sea ice, can have stability problems, and are sometimes trapped in shifting pack ice and lost.

Ice is an important part of the habitat of 25 species of marine mammals that occur in the Bering Sea (Fay, 1974; Burns et al., 1981). It may serve as a substrate, barrier, or to force migrations. Species that regularly come in contact with ice include the following: Polar bear, *Ursus maritimus;* walrus, *Odobenus rosmarus;* harbor seal, *Phoca vitulina;* ringed seal, *P. hispida;* ribbon seal, *P. fasciata;* bearded seal, *Erignathus barbatus;* narwhal, *Monodon monoceros;* beluga whale, *Delphinapterus leucas;* and bowhead whale, *Balaena mysticetus.* For these and other species, the wide views of ice

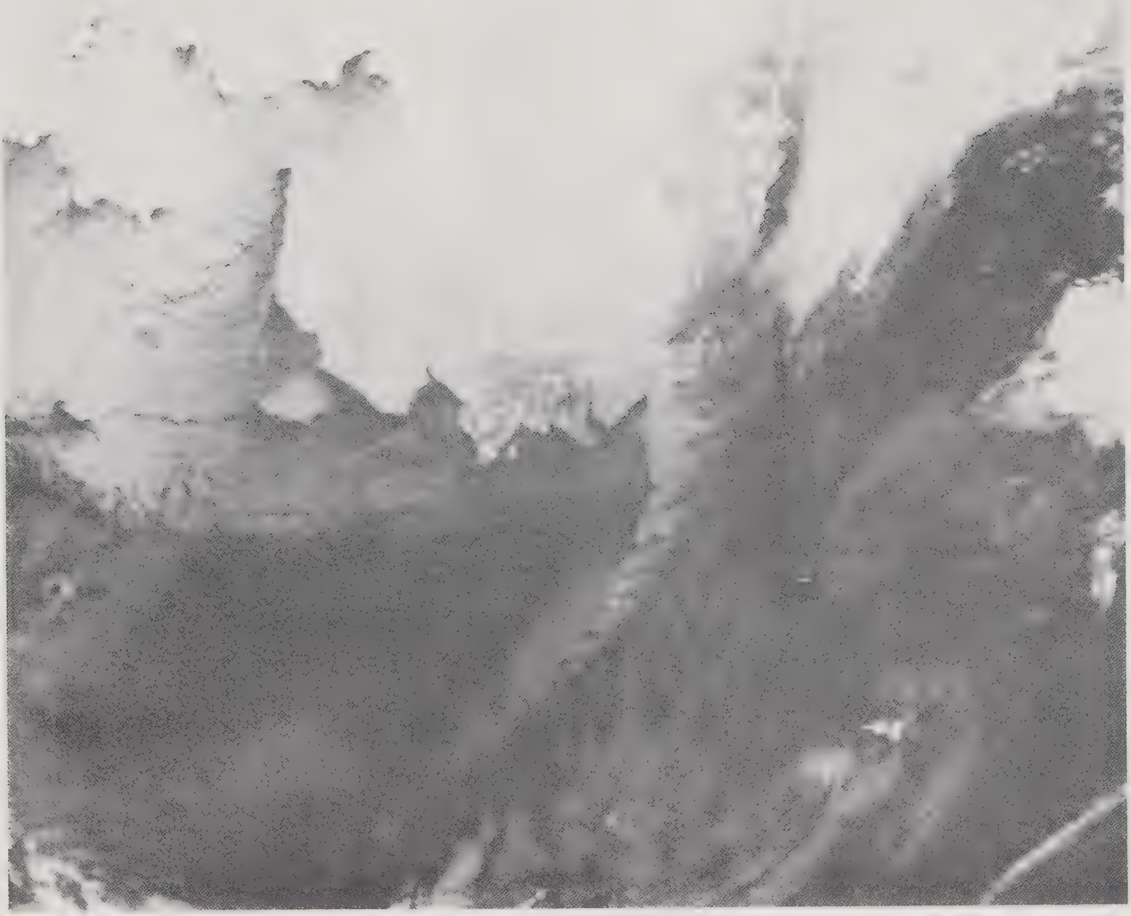

Figure 7. – Ice cover in the eastern Bering Sea, 18 February 1983, NOAA-7 AVHRR channel 4. Ice, clouds, and snow-covered land all appear whiter (colder) than open water. Pack ice extends from the Bering Strait, in the top left corner, past St. Matthew and Nunivak Islands, but does not reach the Alaska Peninsula to the southeast. Photograph courtesy of G. L. Hufford, NOAA/NESDIS, Satellite Field Services Station, Anchorage, Alaska.

characteristics that can be obtained from satellite imagery provide unique information for use in conservation and management.

Migration Routes and Timing

Satellite imagery can provide useful information on environmental conditions related to the routes and timing of long-distance migrations by marine mammals and fish. In the eastern North Pacific and in waters off Alaska, many important species occupy large habitat areas and make extensive seasonal migrations. These large activity areas are often in remote and data-poor regions. Satellite coverage, because of its wide areal views and long-term repeated observations, provides data with time and space characteristics that are appropriate for interpreting large-scale migratory phenomena. Applications include planning research, experimental design, and evaluating strategies for population enumeration.

The North Pacific albacore, *Thunnus alalunga,* performs transpacific migrations and supports important commercial fisheries in the western, central, and eastern North Pacific. Seasonal migration into North American coastal waters is associated with the Transition Zone between Pacific central and subarctic water masses (Laurs and Lynn, 1977). The frontal structure of these waters may affect both the timing and location of the arrival of albacore into the summer fishery along the coast. Figure 8 illustrates CZCS color frontal patterns in the central Pacific that could influence the course of the migration.

The potential for using both color and infrared temperature imagery in

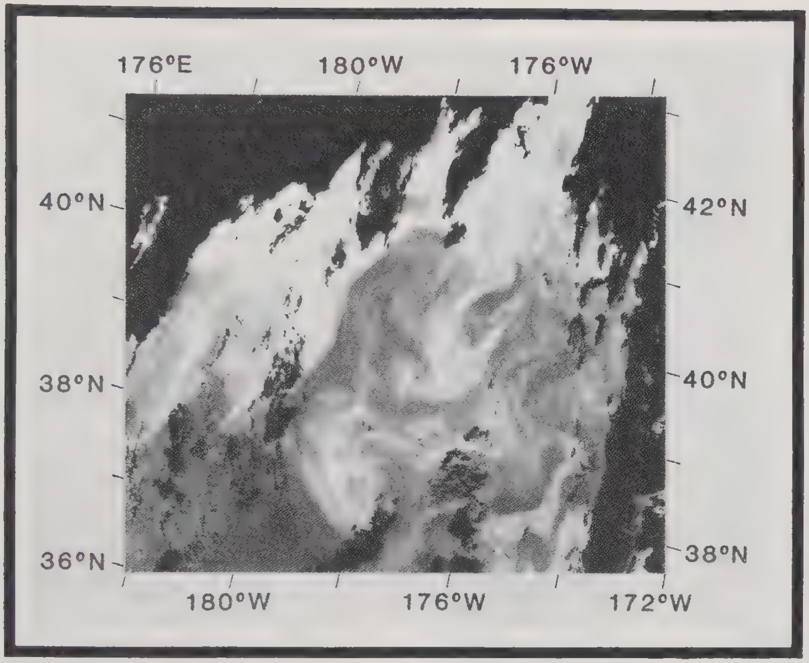

Figure 8.—Phytoplankton pigment concentration in a 600 × 600 km area of the central North Pacific, measured by the Coastal Zone Color Scanner, 30 June 1980. Black = clouds, darkest gray = 0.08 mg m^{-3}, white = 5.7 mg m^{-3}.

fishery operations in these waters has been explored on a limited basis with promising results. Although cloud cover allows only infrequent views of the sea surface, the surface patterns seem to be less dynamic than in coastal waters. Color boundaries are detectable from satellites during all seasons, but pronounced sea surface temperature fronts are not present during summer-autumn due to seasonal warming. However, infrared satellite imagery has been used to locate the subtropical front during winter (Van Woert, 1982) and spring months[3].

In Arctic and subarctic areas, such as the Beaufort Sea and northern Bering Sea, the movements and distribution of sea ice have important influences on the movements of marine mammals. Bowhead and beluga whales make regular seasonal migrations through the shear zones and lead systems that develop in the Arctic pack ice (Braham et al., 1980). In the case of the bowhead whale, the prediction and evaluation of migration paths is important because it is an endangered species and the western Arctic population requires careful annual censusing. Satellite imagery showing ice cover and open-water corridors is used to spot check the sampling design for summer whale counts.

There is potential for similar applications of satellite data in other oceanic and coastal areas, although the relationships between environmental characteristics and marine mammal migrations are not as obvious. For example, the eastern Pacific stock of gray whale, *Eschrichtius robustus,* undergos regular annual migration between summer feeding grounds in the Chukchi Sea and winter breeding grounds in Mexico (Pike, 1962). Satellite coverage of the onset of winter ice cover in the Bering Strait may help explain the environmental signals that initiate the southern migration. Other marine mammals that are important in the region, and that undergo long-distance movements, include: Northern fur seal, *Callorhinus ursinus,* migrating between summer breeding grounds on the Pribilof Islands in the eastern Bering Sea (and on other islands around the Northern Pacific rim) and wintering areas in the Gulf of Alaska and off the U.S. Pacific coast (Fiscus, 1978); humpback whale, *Megaptera novaeangliae,* an endangered species of which the eastern Pacific stock migrates between breeding and calving areas in the Hawaiian Islands and summer feeding grounds in the inland waters of southeastern Alaska (Wolman, 1978); and a number of species of dolphins and porpoise.

Allocation of Sampling Effort

Annual egg and larva surveys of northern anchovy are a regular activity of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Each survey requires 4-5 weeks of ship time to make vertical net tows at 800-900 stations. The accuracy of the estimate of spawning biomass derived from each survey depends on complete coverage of the geographic range of the spawning stock. Without a priori knowledge of this distribution, many extra stations beyond the range limits must be sampled to ensure adequate coverage. We are now investigating the use of satellite imagery to plan egg surveys based on environmental limits characterizing the spawning habitat and detectable from satellites, as described above.

The 1983 survey plan was modified during the cruise using information from satellites. When the cruise began north of Point Conception in February, eggs were found much farther north and offshore than in recent years. Upon examination of AVHRR temperature imagery, we realize that this extension of the spawning range was due to the 1982-83 El Niño event. The cold-water boundary which normally limits

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[3] R. Lynn. 1984. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, Ca 92038. Pers. commun.

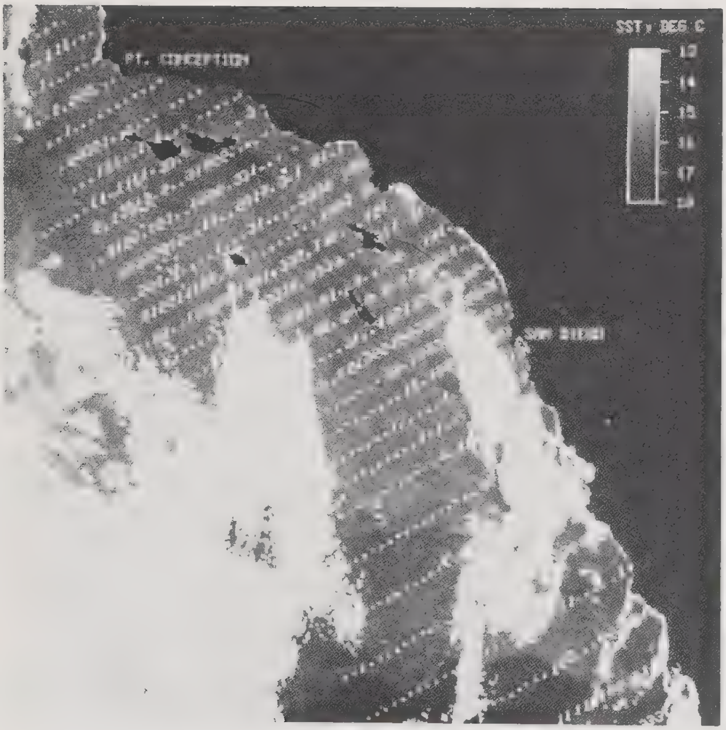

Figure 9.—Northern anchovy egg distribution, 9 February-29 March 1983: • = 0, 1 = 1-3, 2 = 4-12, 3 = 13-229 eggs/0.05 m². Sea surface temperature (°C) from NOAA-7 AVHRR, 10 February 1983.

spawning to the southeast of Point Conception had shifted to the north and offshore (Fig. 9, compare with Fig. 3). As a result, the lines of sampling stations were extended farther offshore than originally planned, to ensure coverage of the entire spawning stock.

In another study conducted in June 1980 on the feeding biology of larval jack mackerel, satellite data were used to locate an intensive sampling grid on a temperature front. The front was observed southwest of San Diego in a NOAA-6 AVHRR image obtained over 1 week prior to the cruise, and it persisted during the sampling period (Fig. 10). The front was subsequently found to be related to an important gradient in food availability[4].

These two examples demonstrate how a single satellite image, from data received and processed in a matter of hours, can save days of ship time by locating significant environmental features and permitting efficient allocation of sampling effort. The potential cost savings are obvious, but the real-time use of satellite data requires facilities for direct reception and processing.

Fisheries Aid Charts

Operational applications of satellite data to commercial fishing activities

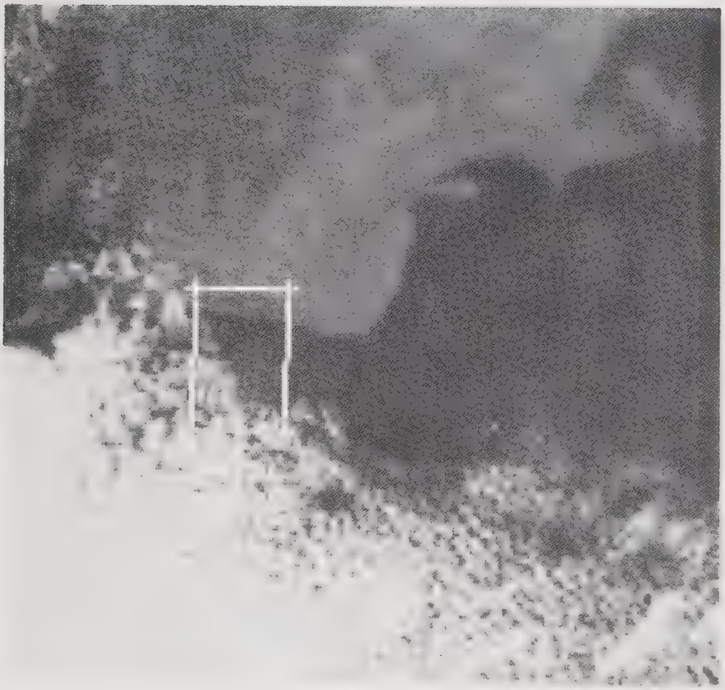

Figure 10.—Uncalibrated NOAA-6 AVHRR channel 4 image off southern California, 5 June 1980. Lighter shades represent cold sea surface temperatures, clouds appear white. Box encloses a 30 × 67 km grid of 41 stations centered at lat. 31° N, long. 120°30′ W.

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[4] R. Hewitt. 1983. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038. Pers. commun.

began along the Pacific coast in 1975 (Breaker, 1981) and have now been extended to Alaska. Charts showing sea surface temperature fronts and sea ice visible in satellite AVHRR images, and surface isotherms mapped from satellite and ship data, are produced routinely by NOAA (Fig. 11). The Northwest Ocean Services Center in Seattle produces a chart covering northern California, Oregon, Washington, and southern British Columbia, from lat. 40°N to lat. 52°N. The Satellite Field Services Station in Redwood City, Calif., produces a chart covering central and southern California and northern Baja California, from lat. 28°N to lat. 40°N. Coverage of both charts extends offshore to long. 135°W. They are produced once or twice weekly year-round and are distributed primarily by radio facsimile from the U.S. Coast Guard

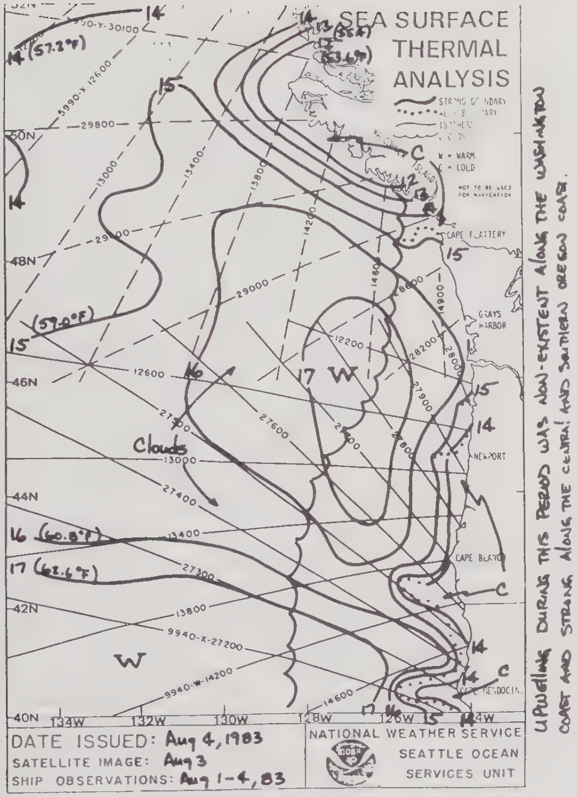
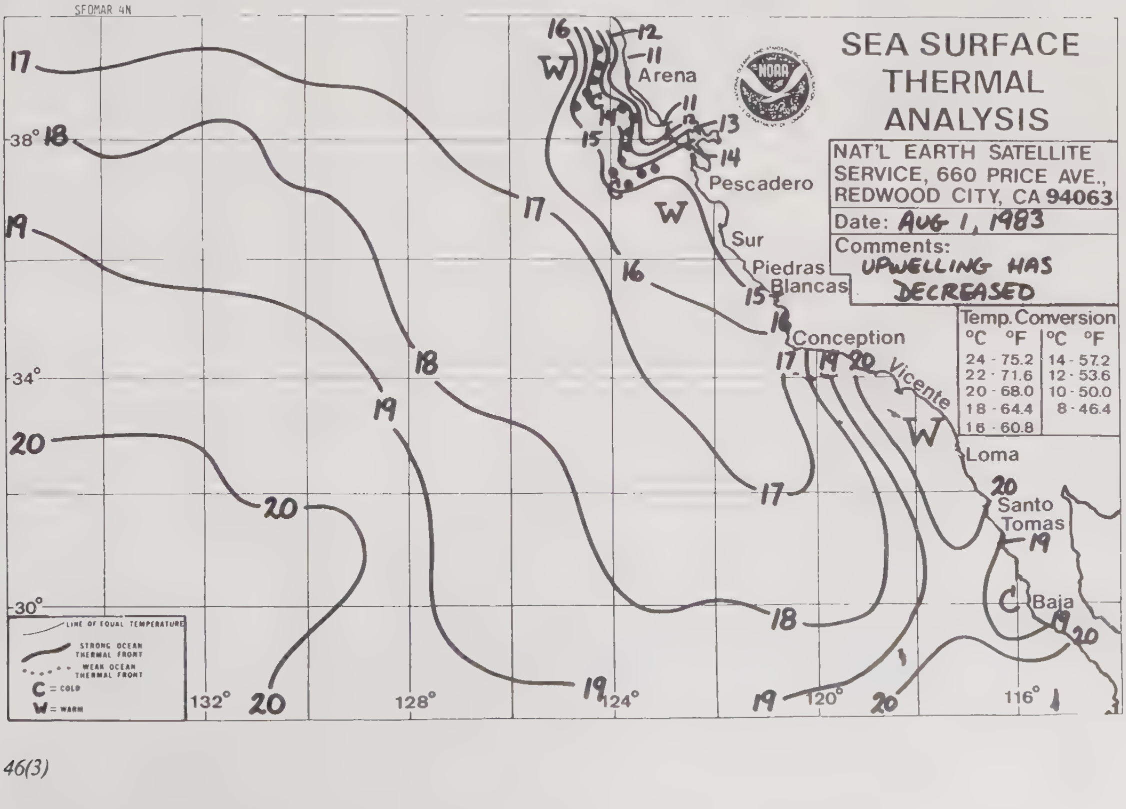

SEA SURFACE THERMAL ANALYSIS
STRONG BOUNDARY
WEAK BOUNDARY
ISOTHERMS
CLOUDS
W = WARM
C = COLD
NOT TO BE USED FOR NAVIGATION
14 (57.3°F)
15 (59.0°F)
16 (60.8°F)
17 (62.6°F)
Clouds
W
17 W
C
CAPE FLATTERY
GRAYS HARBOR
NEWPORT
CAPE BLANCO
CAPE MENDOCINO
50N
48N
46N
44N
42N
40N
134W
132W
130W
128W
126W
124W
DATE ISSUED: Aug 4, 1983
SATELLITE IMAGE: Aug 3
SHIP OBSERVATIONS: Aug 1-4, 83
NATIONAL WEATHER SERVICE
SEATTLE OCEAN SERVICES UNIT
UPWELLING DURING THIS PERIOD WAS NON-EXISTENT ALONG THE WASHINGTON COAST AND STRONG ALONG THE CENTRAL AND SOUTHERN OREGON COAST.

Figure 11.—Sea surface temperature charts produced by the National Weather Service.


SFOMAR 4N
SEA SURFACE THERMAL ANALYSIS
NAT'L EARTH SATELLITE SERVICE, 660 PRICE AVE., REDWOOD CITY, CA 94063
Date: AUG 1, 1983
Comments: UPWELLING HAS DECREASED
Temp. Conversion
°C °F
24 - 75.2
22 - 71.6
20 - 68.0
18 - 64.4
16 - 60.8
14 - 57.2
12 - 53.6
10 - 50.0
8 - 46.4
Arena
Pescadero
Sur
Piedras Blancas
Conception
Vicente
Loma
Santo Tomas
Baja
W
C
38°
34°
30°
132°
128°
124°
120°
116°
LINE OF EQUAL TEMPERATURE
STRONG OCEAN THERMAL FRONT
WEAK OCEAN THERMAL FRONT
C = COLD
W = WARM

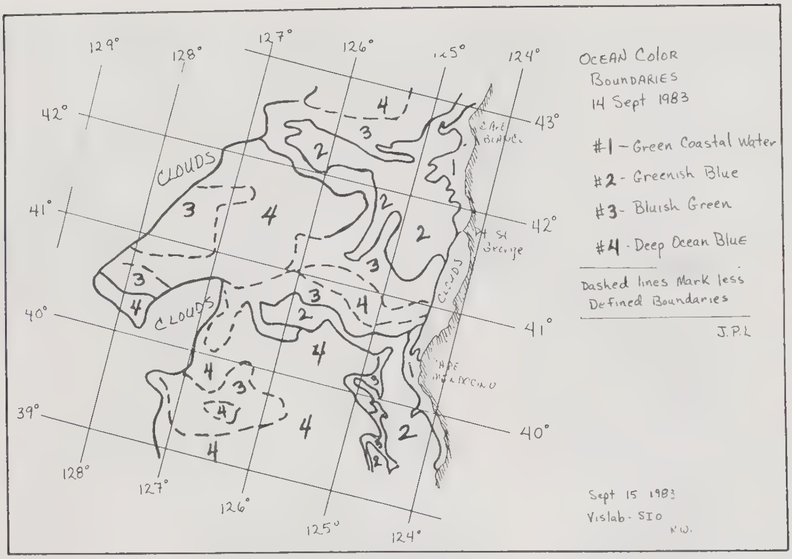


Figure 12.—Ocean color boundary chart off northern California and Oregon (R. Wittenberg, Scripps Visibility Laboratory).

radio station at Point Reyes, Calif. Fishermen use these charts to save time in searching for productive fishing areas associated with frontal features.

The Alaska Ocean Services Unit, located in Anchorage, produces charts covering British Columbia, the Gulf of Alaska, Aleutian Islands, eastern Bering Sea, Chukchi Sea, and Beaufort Sea, from lat. 48°N to lat. 75°N. Charts showing sea surface temperature and sea ice are distributed three times a week; these are intended to aid the safety and efficiency of fishing. Other charts showing 3-and 5-day sea ice forecasts are also distributed daily in winter. Both types of charts are issued by radio facsimile from the U.S. Coast Guard Station at Kodiak, Alaska.

Ocean color boundary charts have been produced experimentally from CZCS data since 1981 in a NASA/Jet Propulsion Laboratory program (Montgomery, 1981). The charts delineate strong gradients in the blue/green color ratio (channel 1/channel 3 radiance). In 1983, charts were produced at almost weekly intervals from May to October (18 charts total), covering coastal areas up to 700,000 km^2 between Vancouver Island, B.C., and Guadalupe Island, Mex. (Fig. 12). A chart was produced only when a large, cloud-free area was located in a Nimbus-7 pass. The chart was then broadcast on the same or following day to fishing boats by radio facsimile from Point Reyes and La Jolla, Calif. Color photographs of the satellite images were distributed by express mail to various fishing ports and to Sea Grant marine advisors in daily contact with fishermen. The color boundary charts and photographs are used by albacore and salmon fishermen. These fish are sometimes found aggregated along color fronts which do not correspond to temperature fronts.

Conclusions

Satellites have altered our perceptions of the ocean environment through the extensive spatial coverage, temporal continuity, and high resolution of the data they provide. Limited, but useful, applications to several types of problems in fisheries research and operations have been demonstrated. Continued development of these and other applications will depend on inexpensive and convenient access to data and data-processing facilities. Recent trends in the federal budget have not been encouraging. For instance, there are no current prospects for a new ocean color scanner to replace the aging CZCS on Nimbus-7. The commercial utility of satellite data depends largely on near real-time availability to fishermen and other maritime users. In the future, this demand may be met by processed satellite data products tailored more to particular user needs.

Acknowledgments

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Feeding ecology of pelagic larvae of English sole *Parophrys vetulus* and butter sole *Isopsetta isolepis* off the Oregon coast

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ABSTRACT: The food habits of the 2 dominant larval pleuronectids off the Oregon coast – English sole *Parophrys vetulus* and butter sole *Isopsetta isolepis* – were analysed. Most specimens were collected during January–April 1971 and March–April 1973. As is typical of larval fishes, *I. isolepis* larvae ingested a variety of prey which changed with increasing fish size. Small larvae fed predominantly on tintinnids, invertebrate eggs, and nauplii, whereas large larvae consumed more copepodite and adult copepods. In contrast, the diet of *P. vetulus* larvae is very specific; appendicularians (*Oikopleura* spp.) comprised 97 % of the total number of food items consumed in 1973. Both *P. vetulus* larvae and appendicularians are most abundant during fall and winter when total zooplankton concentrations off Oregon are low. *I. isolepis* larvae are most abundant during spring when upwelling stimulates productivity. In 1971, seasonal abundance peaks of *P. vetulus* larvae and appendicularians did not coincide. During this year, larvae fed less on appendicularians than in 1973 (66 % of the total number of food items), and more on other food sources such as tintinnids, invertebrate eggs, and nauplii. In 1971 more *P. vetulus* larvae had empty guts than in 1973; this observation suggests increased starvation. In addition, fewer large larvae were present in 1971, perhaps due to higher mortality rates. Hence, in contrast to *I. isolepis* larvae, *P. vetulus* larvae are dependent upon a specific prey; a mismatch of *P. vetulus* and appendicularian abundance peaks may result in significant food-related mortality.

INTRODUCTION

Marine fishes with very high fecundities are characterized by great mortality between egg and adult stages. It is generally agreed that most of this mortality occurs during the first few months in the pelagic larval phase due to starvation and predation (Hunter, 1976); factors causing interannual variability in this mortality may thus affect year-class strength. Hjort (1914, 1926) believed that the most critical factor for larval survival is the availability of planktonic food at the time of complete yolk absorption. High concentrations of an appropriate food must be present or first-feeding larvae may die of starvation after just a few days (Blaxter and Hempel, 1963; May, 1974; Hunter, 1981). In addition, starving larvae are more susceptible to predation, disease, parasites, and unfavorable environmental conditions and are also less efficient at catching prey due to impaired swimming abilities (Laurence, 1972; Blaxter and Ehrlich, 1974; Bailey and Yen, 1983).

Many factors affect the coincidence in timing of abundances of larval fishes and their food sources. Many marine fishes spawn when chances of optimal conditions for larvae are greatest (Cushing, 1975). Maximal food density, however, is not the only factor important to larval survival; water currents may transport planktonic larvae away from favorable areas. Productivity associated with upwelling, for example, may result in high larval food densities, but coincide with detrimental offshore transport away from coastal nursery grounds (Parrish et al., 1981). In the Oregon coastal region, however, offshore larval drift may not be an important factor in year-class strength because coastal and offshore larval assemblages remain dis-

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tinct from year to year under differing conditions of upwelling (Richardson and Pearcy, 1977; Laroche and Richardson, 1979).

Parophrys vetulus and *Isopsetta.isolepis* are the second and third most abundant species in the Oregon nearshore (2 to 28 km from the coast) larval fish assemblage, following osmerids (Richardson and Pearcy, 1977). *P. vetulus* has an extended spawning season, with peak spawning typically from January to March, though spawning peaks may also occur as early as September (Kruse and Tyler, 1983; Mundy, 1984). *I. isolepis* spawns from February through May (Richardson et al., 1980); thus the larvae of these 2 species co-occur during only part of their pelagic phases.

The development of *Parophrys vetulus* and *Isopsetta isolepis* from egg to benthic juvenile is similar. Larval *P. vetulus* hatch from pelagic eggs in 4 to 12 d, depending upon temperature (Alderdice and Forrester, 1968), at 2.7 to 2.9 mm notochord length. Metamorphosis to the benthic form occurs between 50 and 120 d, at 18 to 22 mm standard length (Laroche et al., 1982; Rosenberg and Laroche, 1982). *I. isolepis* larvae hatch about 6 d after fertilization, at 2.7 to 2.9 mm notochord length (Richardson et al., 1980). Transformation to the benthic juvenile is complete at about 21 mm standard length.

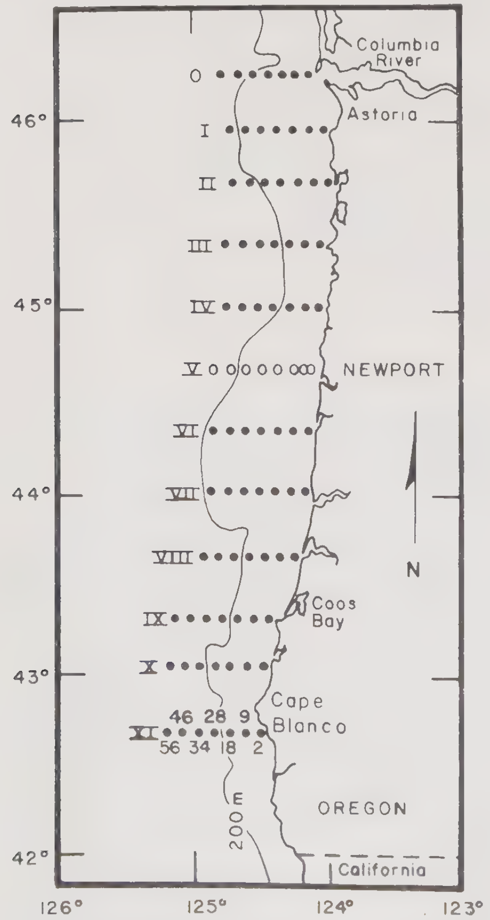

Fig. 1. Sampling stations off Oregon, USA. Numbers along Transect XI: km from shore. Open circles at Transect V: Newport Hydroline (NH; from Laroche and Richardson, 1977)

Laroche and Richardson (1979) observed year-to-year temporal and spatial variations in Oregon coastal larval fish abundances which may reflect ultimate year-class strengths of the cohorts (Hayman and Tyler, 1980). These variations are due to changes in peak spawning times and durations, as well as biotic and environmental factors influencing larval survival. During winter off the Oregon coast, one of the most important factors may be food availability. In this region, summer upwelling results in increased primary production and greater summer larval food abundances (Small et al., 1972; Peterson and Miller, 1977). Because *Parophrys vetulus* spawns during fall and winter, larval food availability may be the most critical factor affecting subsequent year-class strength. In addition, when the morphologically similar larvae of *P. vetulus* and *Isopsetta isolepis* co-occur during winter, competition for the same limited food sources may further affect survival. This has been shown for larval cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* in laboratory experiments (Laurence et al., 1981). In the present study we describe the feeding ecology of the pelagic larval stages of *P. vetulus* and *I. isolepis* in order to improve understanding of the causes of variability in year-class strength.

METHODS

Sample selection

Larvae were selected from curated ichthyoplankton survey samples collected off the coast of Oregon from 1971 to 1975 (Richardson and Pearcy, 1977; Laroche and Richardson, 1979). From January 1971 through August 1972, collections were made along the Newport Hydrographic (NH) line (on 44°40′ N, 2–111 km off Newport, Oregon (Fig. 1; Richardson and Pearcy, 1977). The hydroline number (NH1, NH3, etc.) refers to the number of nautical miles from the coast.

During March and April of 1972 and 1973, and during March of 1974 and 1975, samples were taken on a coastal grid 2 to 56 km offshore from the Columbia River to Cape Blanco, Oregon (Fig. 1; Laroche and Richardson, 1979). On all cruises, plankton was collected in 70 cm bongo nets with 0.571 mm mesh. Tows were stepped or straight oblique from the bottom or from 150 m to the surface when depth exceeded 150 m. Samples were preserved in 5 % formalin buffered with sodium borate.

Initially, 380 *Parophrys vetulus* larvae and 361 *Isopsetta isolepis* larvae were examined from March and April of 1973. That year was chosen because there were sufficient larvae of both species in relatively broad size ranges. These larvae provided the major source of data. For comparison, however, 183 *P. vetulus* larvae from January through April 1971, 52 *I. isolepis* from June 1971, and 25 *I. isolepis* from June 1972 were also examined. This increased the number of large *I. isolepis* and small *P. vetulus* since these 2 size categories were limited in the 1973 samples. No *P. vetulus* larvae greater than 15.9 mm SL were examined from 1971 because few larger larvae were collected that year.

A sample was selected for examination if it contained at least 10 specimens of either species. Usually, about 10 *Parophrys vetulus* and/or 10 *Isopsetta isolepis* larvae from each selected sample were examined. Fewer than 10 were examined from some samples, however, because of deterioration or more than 10 were examined if they were available. When sorting a sample, the first 10 larvae encountered with intact guts were removed. Where a broad size range was present, however, larvae were selected to obtain the widest possible size spectrum from each sample.

Parophrys vetulus larvae examined from 1973 were from 38 samples collected on 13 d (17 Mar to 20 Apr). *Isopsetta isolepis* larvae from 1973 were from 30 samples from 13 d (17 Mar to 26 Apr). *I. isolepis* and *P. vetulus* larvae co-occurred in 19 of these samples. All samples (except 1) were collected at stations 1, 5, 10, 15, and 20 nautical miles off the Oregon coast. Samples examined from 1973 were collected at a variety of day and night times to investigate diel feeding patterns. Larvae examined from other years were chosen from day collections (0800 to 1800) to maximize feeding incidence. *P. vetulus* larvae from 1971 were from 13 samples on 7 d (6 Jan to 22 Apr). *I. isolepis* larvae from 1971 and 1972 were selected from single dates because these were the only days that large larvae were taken during daylight hours; larvae from 1971 were from 5 samples taken 28 June; those from 1972 were from 3 samples taken 11 June.

Laboratory techniques

Larval dissection techniques followed Arthur (1976). Briefly, specimens were placed in glycerin, soaked overnight, and examined on a microscope slide. Standard length (snout tip to notochord tip until full notochord flexion, then to the posterior edge of the hypurals) and mouth width (horizontal distance from a frontal view) were measured to the nearest hundredth of a millimeter. Small *Parophrys vetulus* and *Isopsetta isolepis* larvae have a straight gut, which begins to coil at about 4 mm standard length (SL) at which time the gut can be roughly divided into fore, mid, and hindgut areas. The entire gut was removed, placed in glycerin, teased open, and the contents removed; the location of major food items was noted. Food items were counted, measured, and identified to the lowest possible taxon.

Gut content analysis

To facilitate analysis, food items were classified into categories characterized by taxon and/or size. For example, copepodites-copepods were classified as a species with a known size (*Pseudocalanus* sp., *Oithona* spp., etc.), or classified as unidentified but of a certain size range (cephalothorax length about 0.25, 0.50, 0.75, or 1.00 mm). Since in many cases, an animal was dorsoventrally or laterally flattened, and only length could be accurately measured, a cephalothorax length to width (widest part of the carapace excluding appendages) ratio was calculated for major copepod species. Unidentified copepodites-copepods were assumed to have a width one-third of their cephalothorax length.

Three parameters were subjectively recorded as follows: (A) stomach fullness: 0: empty, 1: ¼ full, 2: ½ full, 3: ¾ full, and 4: full; (B) digestive stage: 1: food present in undigested condition, 2: food somewhat digested, and 3: food very digested; (C) gut diameter: 1: narrow, 2: average, and 3: distended.

For the various larval length groups, percent by number (% N) and percent frequency of occurrence (% F) were tabulated. The % N is the percentage of the total number of prey items, while % F is the percent frequency of occurrence of a food item among larvae with food in their guts. The volume of a prey item was calculated assuming it to be a spheroid, by the formula $^{1}/_{6}$ [π (length) (width)^2]. The mean prey width for each larval length group was calculated by summing the individual widths of each prey item ingested in that length group, and dividing by the total number of prey items ingested. Mean prey volume was calculated in a similar manner.

Appendicularians were common prey items and were studied in more detail. They are usually found in the gut digested except for characteristic spheroid fecal pellets. To establish a relationship between appendicularians and their fecal pellets, 202 appendicularians (*Oikopleura* spp.) randomly chosen from nearshore Oregon plankton samples were examined. The mean number of fecal pellets per appendicularian was calculated, and used to determine the number of appendicularians ingested based on the number of fecal pellets found in a larval fish gut, after Shelbourne (1962). In addition, fecal pellet length to appendicularian trunk length and width were regressed, and confidence limits were determined. Fecal pellets from larval fish guts were measured and classified into eight 0.05 mm length groups with median lengths of 0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, and 0.40 mm, and the results were used to calculate ingested appendicularian size, following Shelbourne (1962).

RESULTS

Variations in feeding

More *Isopsetta isolepis* and *Parophrys vetulus* larvae from daytime samples had food in their guts than did those from nighttime samples (Fig. 2 and 3). After midnight, the percentage of larvae with empty guts increased rapidly, particularly for *P. vetulus*. In addition, food found in *P. vetulus* and *I. isolepis* guts during early morning was always very digested and often in the posterior portion of the gut. Many larvae which had empty guts between 0200 and 0600 had very narrow guts, although empty but distended guts were also found. After 0600, the percentage of larvae with food in their guts increased rapidly and remained over 80 % throughout the day.

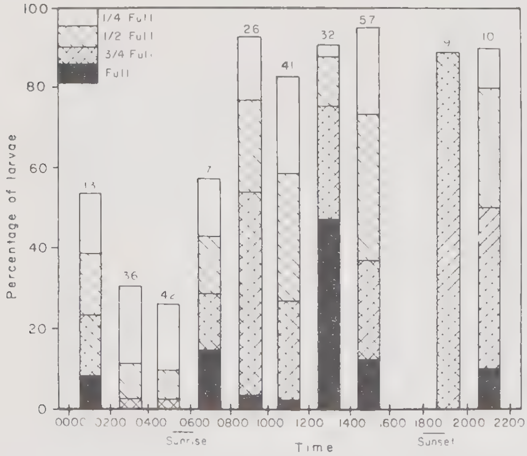

Fig. 2. *Isopsetta isolepis*. Diel variations in gut fullness of larvae from March and April, 1973. From the top of a bar to 100 % represents the percentage of empty guts. Numbers above bars: numbers of larvae examined from that time period. Only larvae 6.0 to 17.9 mm SL are considered because smaller larvae have a higher percentage of empty guts which would bias the results

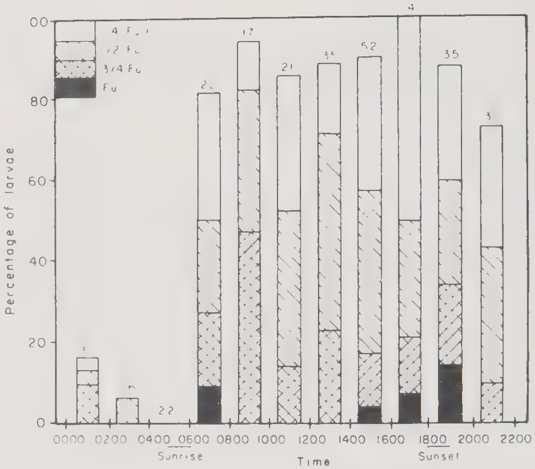

Fig. 3. *Parophrys vetulus*. Diel variations in gut fullness of larvae from March and April, 1973. From the top of a bar to 100 % represents the percentage of empty guts. Numbers above bars: numbers of larvae examined from that time period. Only larvae 6.0 to 17.9 mm SL are considered because smaller larvae have a higher percentage of empty guts which would bias the results

In both years, there were ontogenetic variations in gut fullness; smaller larvae had higher incidences of empty guts than larger larvae (Fig. 4; Tables 1, 2, and 3). For clarity, only larvae from daytime samples (0800 to 1800) were considered in Fig. 4 since larvae of all sizes from nighttime samples have more empty guts than from daytime samples. More *Parophrys vetulus* larvae collected during 1971 had empty guts than in 1973; all *P. vetulus* larvae below 5 mm SL examined from 1971 had empty guts. All *Isopsetta isolepis* larvae examined from 1971 and 1972 were greater than 10 mm SL, and almost all had food in their guts (Table 2). In addition, the mean numbers of food items per feeding larva were high in these years compared to *I. isolepis* from 1973 (Table 1). In all years, *I. isolepis* larvae have a higher maximum and mean number of items in their guts than do *P. vetulus* larvae (Tables 1, 2, and 3).

Diet composition

Isopsetta isolepis. Food items in the guts of larvae were usually in good condition. Crustaceans generally had exoskeletons intact, but tissues digested. Only rarely did prey appear to have been just eaten. In addition, prey were rarely extremely digested and crushed, except in early morning hours (about 0200 to 0600). Food was typically found mainly throughout the midgut and hindgut regions. Food in the hindgut did not generally appear to be more digested than in the midgut. Although there were differences in diet

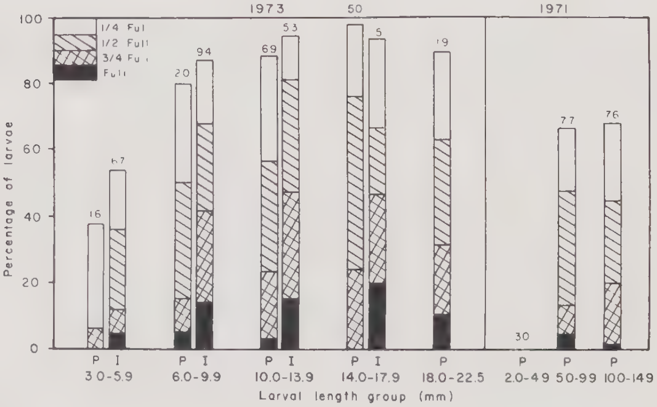

Fig. 4. *Parophrys vetulus* (P) and *Isopsetta isolepis* (I). Ontogenetic variations in gut fullness of larvae from 1973 and 1971. From the top of a bar to 100 % represents the percentage of empty guts. Numbers above bars: numbers of larvae examined from each length group. Only larvae from daytime samples (0800 to 1800) are considered

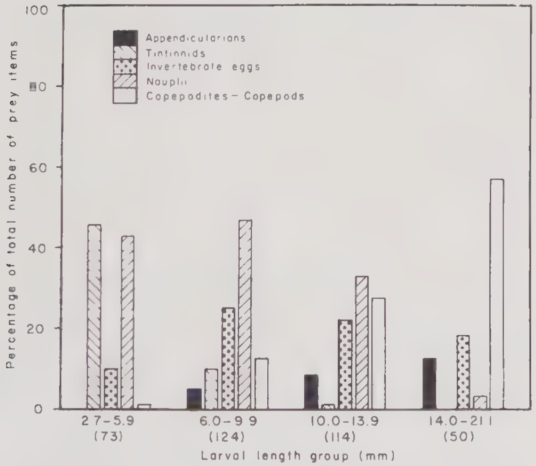

Fig. 5. *Isopsetta isolepis.* Diet composition of major prey items of larvae from 1973. Numbers in parentheses: numbers of larvae examined from each length group

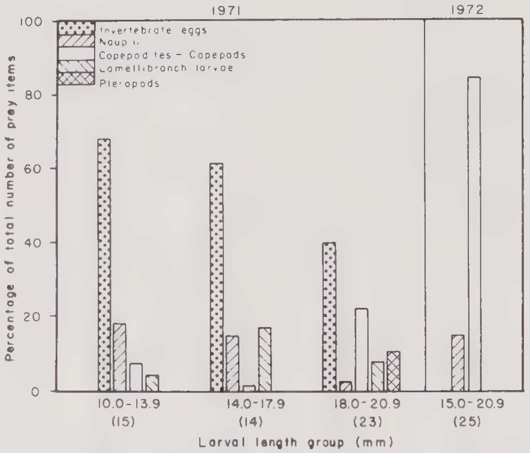

Fig. 6. *Isopsetta isolepis.* Diet composition of major prey items of larvae from 1971 and 1972. Numbers in parentheses: numbers of larvae examined from each length group

between years, no consistent differences were detected between stations within a year. Most guts contained a variety of prey types.

Larvae had a varied diet in 1973 (Fig. 5). Small larvae ingested primarily tintinnids (0.05 mm) and nauplii (0.10 to 0.35 mm, mainly of copepods). With increasing larval size, tintinnids were replaced by larger prey such as copepodite and adult copepods (0.25 to 1.20 mm cephalothorax length); also, nauplii lost importance in the diet above 14 mm SL. The major copepods ingested were *Pseudocalanus* spp. (Table 1). Invertebrate eggs (0.05 to 0.30 mm), many of them *Calanus marshallae* (0.20 mm), were frequently consumed throughout ontogeny. Appendicularians are also a significant prey item, particularly at larger sizes.

Since only 5 larvae greater than 18 mm SL with stomach contents were available for examination from 1973 (Table 1), larger larvae were examined from 2 other years, 1971 and 1972 (Fig. 6, Table 2). During 1971, invertebrate eggs were the dominant food source for all larvae examined. As in 1973, nauplii were important in the diet of smaller larvae, and copepodite and adult copepods gained importance with increasing larval size. The 2 species of copepod ingested in 1971, however, were *Acartia longiremis* and the harpacticoid *Microsetella rosea*. Also in contrast to 1973, lamellibranch larvae and pteropods were important diet items in 1971. During 1972 larvae greater than 15 mm SL had a less varied diet than in the other years, ingesting almost exclusively nauplii, copepodites and adult copepods (mainly *Acartia longiremis, Pseudocalanus* sp. and *Oithona* spp.).

Table 1. *Isopsetta isolepis.* Diet composition of larvae from 1973. Numbers in parentheses: percentages by number of a prey species in the previous major category. % N = percentage of the total number of prey items; % F = percent frequency of occurrence

Prey items	Larval length groups (mm)								
	2.7–5.9		6.0–9.9		10.0–13.9		14.0–17.9		18.0–21.1
	% N	% F	% N	% F	% N	% F	% N	% F	% N
Tintinnids	45.5	47.5	10.0	15.4	1.2	3.8	.9	4.3	
Invertebrate eggs	10.0	35.0	25.0	46.2	22.1	33.3	24.0	21.7	
Unidentified	(50.0)		(40.8)		(80.6)		(100)		
Calanus marshallae	(50.0)		(59.2)		(19.4)				
Nauplii	42.6	70.0	46.6	73.6	32.7	44.9	4.2	13.0	
Copepodites-copepods	1.0	5.0	12.6	16.5	27.4	60.3	49.3	60.9	87.8
Unidentified	(100)		(87.1)		(55.1)		(37.7)		(41.3)
Calanoid									
Pseudocalanus spp.			(6.5)		(32.1)		(56.8)		(55.2)
Paracalanus spp.			(3.2)		(2.2)		(1.8)		(3.4)
Ctenocalanus spp.					(.7)		(1.8)		
Cyclopoid									
Oithona spp.			(3.2)		(9.9)		(1.8)		
Appendicularians			5.0	8.8	8.4	10.3	15.0	21.7	3.0
Polychaete larvae			1.0	3.3	5.3	17.9	5.1	13.0	9.1
Euphausiid calyptopis					1.4	7.7	1.7	8.7	
Unidentified					2.7	5.5			
No. of larvae examined	73		124		114		37		13
No. with prey	40		86		75		22		5
Maximum no. of prey items per larvae	19		29		24		20		18
Mean no. of prey items per feeding larvae from day samples	5.3		9.4		6.4		7.2		7.0

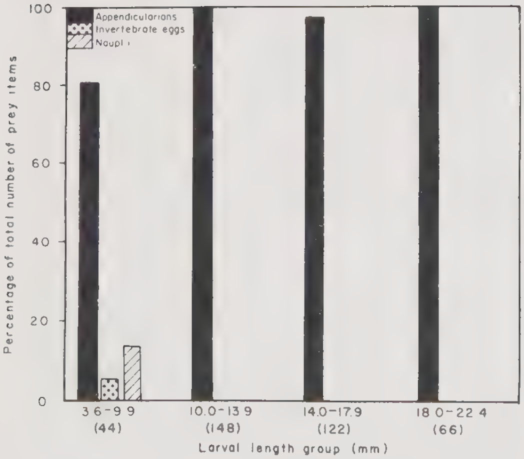

Fig. 7. *Parophrys vetulus.* Diet composition of major prey items of larvae from 1973. Numbers in parentheses: numbers of larvae examined from each length group

Parophrys vetulus. The diet of larvae in 1973 was very different from that of *Isopsetta isolepis* larvae (Fig. 7; Table 3). Appendicularians (*Oikopleura* spp.) were consumed almost exclusively. Only larvae smaller than 10 mm SL ingested a few nauplii and invertebrate eggs. Appendicularians were almost always found in the gut as highly digested remains, which consisted of spheroid oblong brown fecal pellets surrounded by a clear matrix and sometimes the trace of a trail. Only rarely were appendicularians in perfect, undigested condition; in these cases they were in the esophagus. Generally, however, food items were not found in the esophagus or foregut region, and were instead located throughout the mid and hindgut regions.

In 1971 (Fig. 8; Table 3), appendicularians still dominated the diet of larvae greater than 5 mm SL. Tintinnids, invertebrate eggs, and nauplii, however, were ingested to a greater extent than in 1973. No differences in diet in relation to station were apparent for larvae collected from either year.

Larval-prey size relation

Mean prey width increased with larval fish size for both *Isopsetta isolepis* (Fig. 9) and *Parophrys vetulus* (Fig. 10). The minimum width of food ingested remained relatively constant for *P. vetulus* and *I. isolepis*, as did the maximum width of food for both species above 14 mm SL. For both species, the maximum prey size ingested was less than the size of prey the larvae apparently could have engulfed, particularly at larger fish sizes, as is indicated by the differ-

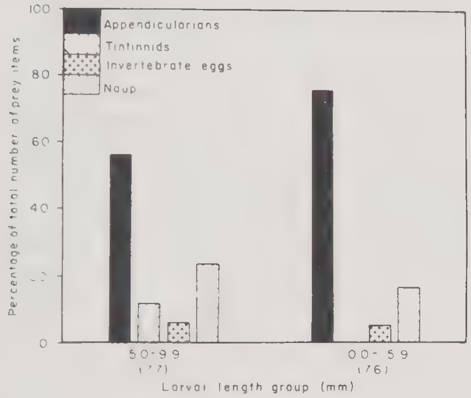

Fig. 8. *Parophrys vetulus.* Diet composition of major prey items of larvae from 1971. Numbers in parentheses: numbers of larvae examined from each length group

ence between fish mouth width and maximum prey width.

For *Isopsetta isolepis,* however, mean prey size increased more than mean prey width indicates, since with ontogeny prey items change from sphere-like forms (tintinnids, invertebrate eggs, nauplii) to more elongated spheroids (copepodites-copepods). Thus, mean prey volume increased more with larval length increase than did mean prey width (Fig. 9).

Appendicularian size relation

The 202 appendicularians (*Oikopleura* spp.) examined from plankton-net collections had a mean of 2.67 fecal pellets with a maximum of 5. This was similar to Shelbourne's (1962) value of 2.65. Only 5 of the 202 appendicularians did not contain fecal pellets, and 78 % had 2 or 3. A relation was established between size of *Oikopleura* spp. and size of their fecal pellets; generally, the larger the appendicularian, the larger the fecal pellets (appendicularian trunk length = 0.23 mm + 2.98 [fecal pellet length], $r^2 = 0.78$; appendicularian trunk width = 0.12 mm + 1.79 [fecal pellet length], $r^2 = 0.70$).

The guts of small *Parophrys vetulus,* from 1973 contained a greater percentage of small fecal pellets; thus, ingested appendicularian size increased with larval

Table 2. *Isopsetta isolepis.* Diet composition of larvae from 1971 and 1972. Numbers in parentheses: percentages by number of a prey species in the previous major category. % N = percentage of the total number of prey items; % F = percent frequency of occurrence

Prey items	Larval length groups (mm)							
	1971						1972	
	10.0–13.9		14.0–17.9		18.0–20.9		15.0–20.9	
	% N	% F	% N	% F	% N	% F	% N	% F
Invertebrate eggs	68.0	80.0	61.3	50.0	40.0	22.7		
Nauplii	18.2	60.0	14.9	57.1	2.7	9.1	15.2	58.3
Copepodites-Copepods	7.6	53.3	1.6	28.6	22.2	40.9	84.5	100.0
Unidentified							(59.0)	
Calanoid								
Acartia longerimis	(100)		(75.0)		(58.6)		(15.7)	
Pseudocalanus spp.							(6.2)	
Paracalanus spp.							(.3)	
Cyclopoid								
Oithona spp.							(18.8)	
Harpacticoid								
Microsetella rosea			(25.0)		(41.4)			
Lamellibranch larvae	4.4	20.0	17.3	35.7	8.1	18.2		
Pteropods			.4	7.1	10.8	31.8		
Polychaete larvae	1.3	20.0	3.2	50.0	9.7	59.1		
Cumaceans			.8	7.1	2.7	13.6		
Appendicularians	.4	6.7			.5	4.5	.3	8.3
Worms			.4	7.1	2.2	9.1		
Amphipods					.5	4.5		
No. of larvae examined	15		14		23		25	
No. with prey	15		14		22		23	
Maximum no. of prey items per larva	44		45		62		39	
Mean no. of prey items per feeding larva from day samples	15.0		17.7		8.4		25.5	

Table 3. *Parophrys vetulus.* Diet composition of larvae from 1971 and 1973. Numbers in parentheses: percentages by number of a prey species in the previous major category. % N = percentage of the total number of prey items; % F = percent frequency of occurrence

	Larval length groups (mm)												
	1971					1973							
Prey items	2.7–4.9	5.0–9.9		10.0–15.9		3.6–9.9		10.0–13.9		14.0–17.9		18.0–22.4	
	% N	% N	% F	% N	% F	% N	% F	% N	% F	% N	% F	% N	% F
Appendicularians		56.5	75.5	76.1	96.2	80.8	84.6	100.0	100.0	97.2	98.6	100.0	100.0
Invertebrate eggs		6.2	18.9	5.4	11.3	5.6	3.9			1.1	2.7		
Unidentified		(8.3)		(10.0)		(100)				(100)			
Calanus marshallae		(91.7)		(90.0)									
Nauplii		23.8	41.5	16.8	13.2	14.0	15.4						
Copepodites-Copepods		1.6	3.8	1.1	1.9								
Tintinnids		11.9	3.8							1.1	1.4		
Polychaete larvae				.5	1.9					.6	1.4		
No. of larvae examined	30	77		76		44		148		122		66	
No. with prey	0	53		53		26		110		73		34	
Maximum no. of prey items per larva		23		14		5		6		16		11	
Mean no. of prey items per feeding larva from day samples		3.6		3.5		1.7		1.1		2.3		3.4	

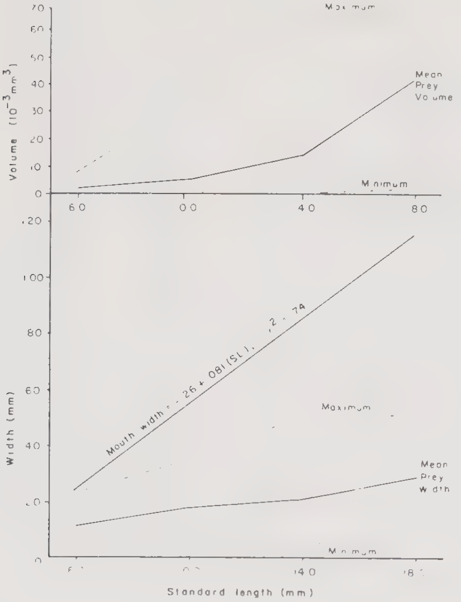

Fig. 9. *Isopsetta isolepis.* Relation between 1973 larval size (n = 361) and mean, minimum and maximum widths and volumes of their prey items as a function of larval standard length. Mouth width indicates maximum size of potential prey

size (Fig. 10). Larvae larger than 14 mm SL, however, contained a range of fecal pellets from the smallest (0.05 mm) to the largest (0.40 mm).

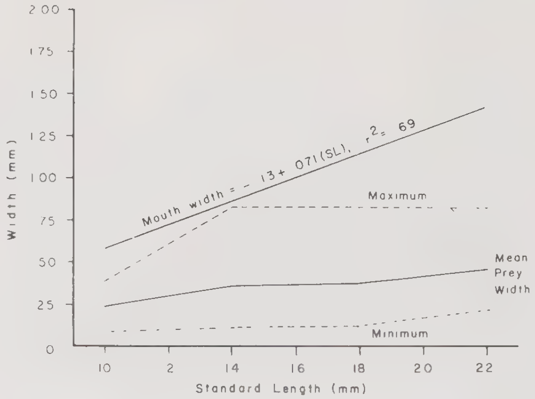

Fig. 10. *Parophrys vetulus.* Relation between 1973 larval size (n = 380) and mean, minimum and maximum widths of their prey items as a function of larval standard length. Mouth width indicates maximum size of potential prey

DISCUSSION

Both *Parophrys vetulus* and *Isopsetta isolepis* larvae displayed a pattern of diurnal feeding typical of larval fishes (Fig. 2 and 3), which generally are visual feeders (Bainbridge and Forsyth, 1971; Arthur, 1976; Last, 1978a, b, 1980; Cohen and Lough, 1983). More *P. vetulus* than *I. isolepis* guts were empty during late night (0200 to 0600), apparently because of the higher digestibility of appendicularians, which lack the hard exoskeletons of copepods.

Ontogenetic variations in feeding incidence were also observed for both *Parophrys vetulus* and *Isopsetta isolepis;* more small larvae had empty guts during daylight hours. Upon capture and fixation regurgitation may be more common at small sizes of larval flatfishes due to the straight gut. The more complex coiled gut at larger sizes could hinder regurgitation (Sherman et al., 1981). Another possibility is an ontogenetic change in feeding success. Small larvae, particularly first feeding larvae, require higher prey concentrations of a more limited size range (0.04 to 0.10 mm) than larger larvae (Hunter, 1981). Small larvae have a shorter perceptive distance, which, combined with slower swimming speeds, results in low searching rates (Hunter, 1972; Houde and Schekter, 1981).

Isopsetta isolepis larvae had a varied diet (Fig. 5 and 6; Tables 1 and 2). The major food sources of *I. isolepsis* are various copepod life stages, which is also true for larval clupeids, engraulids, carangids, gadids, merluciids, sciaenids, and others (Bainbridge and Forsyth, 1971; Arthur, 1976; Last, 1980; Sumida and Moser, 1980; Govoni et al., 1983). An ontogenetic change in diet composition, with smaller larvae ingesting more small prey items, such as tintinnids and nauplii, is also displayed by these species, and by *I. isolepis* larvae in this study. As size increases, ingestion of larger prey is necessary for the growth and survival of fish larvae (Howell, 1973; Hunter, 1977).

The maximum size prey which can be ingested is determined by larval mouth size (Shirota, 1970). Prey width, not length, is the critical measurement in determining prey size limitations because fish larvae usually engulf oblong prey (such as copepods) head first (Hunter, 1981). Thus, the maximum size of prey ingested by *Isopsetta isolepis* larvae in this study is well below the maximum possible size (Fig. 9). This is a trend commonly observed in other species of larval fish (de Mendiola, 1974; Arthur, 1976; Last, 1978a, b; Sumida and Moser, 1980). Carapace width of copepods may not be a good functional measurement because appendages are not considered. Small, easily captured prey may be preferable to faster moving large prey, resulting in size selectivity due to differential capture probabilities (Drenner et al., 1978).

Prey abundances in the plankton also influence larval diet. The 2 major copepod species ingested by *Isopsetta isolepis* differed between years (Tables 1 and 2), but were of similar sizes, about 1 mm cephalothorax length. In 1973, the primary species was *Pseudocalanus* sp., whereas in 1971, *Acartia longiremis* was dominant. Off the Oregon coast, copepods are the most abundant component of the zooplankton at all times (Peterson and Miller, 1975, 1976, 1977). The most common coastal species in both winter and summer is *Pseudocalanus* sp., and in summer *Acartia longiremis* ranks second in abundance. Thus, *I. isolepis* larvae are ingesting common zooplankton types, although it is not possible to speculate about feeding selectivity without coincident sampling of larvae and their food sources.

In contrast to *Isopsetta isolepis, Parophrys vetulus* larvae have a very specific diet, composed of 97 % appendicularians in 1973 (Fig. 7; Table 3). Thus, competition between the larvae of both species for the same food resources during their pelagic phase is largely avoided. Appendicularians are a major diet component of a number of other pleuronectiform species also, including *Glyptocephalus cynoglossus, Arnoglossus laterna, Microstomus kitt* (Last, 1980), and *Pleuronichthys cornutus* (Kuwahara and Suzuki, 1983). The larval flatfish species best known for ingesting appendicularians (notably *Oikopleura dioica*) is the plaice *Pleuronectes platessa* (Shelbourne, 1953, 1957, 1962; Ryland, 1964; Wyatt, 1974; Last, 1978a). The diet of larger *P. platessa* larvae is composed of a larger percentage of appendicularians, often as high as 100 %. Similar to the current work, Shelbourne (1962) showed a size relation between larval predator and appendicularian prey.

Some species of non-pleuronectiform larvae also ingest appendicularians. Appendicularians often are a major component of the diet of larval sand eels *Ammodytes marinus* in the North Sea (Ryland, 1964; Wyatt, 1974). In addition, larvae of the chub mackerel *Scomber japonicus* were found to ingest 63.7 to 100 % appendicularians in the southeastern Pacific (Lipskaya, 1982). Given the rapid digestion and difficulty in identifying remains, however, appendicularians may be an even more important component of larval fish diets than gut content analysis indicates.

Smaller *Parophrys vetulus* larvae in this study consumed more non-appendicularian food items than larger larvae, perhaps due to the feeding limitations of small larvae. There also may not be adequate concentrations of very small appendicularians to support small larvae; the size composition of appendicularians off the Oregon coast is unknown. The upper size limit of appendicularians ingested by *P. vetulus* larvae, however, is within the upper size range of appendicularians common off Oregon, as determined by the appendicularians from plankton samples examined in the current work.

In the Oregon coastal region, appendicularians (mainly *Oikopleura* spp.) are most abundant in fall and winter. In surveys conducted by Peterson and Miller (1976) off Oregon from June 1969 through July 1972, appendicularians represented a mean of 5.7 % of the total winter zooplankton catch. *Oikopleura* showed clear peaks of abundance, however, with 60 % or greater of the total yearly density taken in a single month and zero catches during the majority of the year. Appendicularians were rarely observed in areas of active upwelling. Although zooplankton surveys were not conducted off Oregon in 1973, winter zooplankton abundance peaks (approximately an order of magnitude less than abundance peaks during the productive summer season) are common, and occurred in all 3 y of the study by Peterson and Miller (1976). The winter of 1973 was mild with low amounts of cloud cover and light winds (Laroche and Richardson, 1979). These conditions are the prerequisites for higher plankton densities resulting from increased sunlight and water column stability (Lasker, 1975, 1978). Thus, the winter of 1973 was potentially a period of high appendicularian abundances.

Water-column stability may be a major factor in increasing zooplankton patch densities during certain times of the year. Upwelling is necessary to replenish surface nutrients, but upwelling and storms may disrupt larval food aggregations, resulting in homogeneous, but lower densities (Lasker, 1975, 1978). Indeed, Hayman and Tyler (1980) have suggested that larval feeding conditions in 1961, the strongest year-class of *Parophrys vetulus* on record off Oregon, may have been promoted by high storm frequency but low average wind speed. Laboratory work on some species suggests that the densities found in the field are rarely sufficient to support high survival (Hunter, 1972; Lasker, 1978); small scale patchiness has been cited as a potential mechanism to account for this discrepancy (Hunter, 1981; Owen, 1981). Appendicularians are known to be patchily distributed. They have been observed to aggregate in parallel slicks, referred to as windrows, which may be formed during periods of mild winds due to wind-wave interaction resulting in Langmuir vortices (Owen, 1966; Allredge, 1982). On days of more intense winds, Alldredge (1982) found appendicularians to be more dispersed due to wind induced chop; thus water column stability may be an important factor in maintaining this system.

In 1971, the appendicularian abundance peak preceded that of *Parophrys vetulus* larvae by several months (Fig. 11; Peterson and Miller, 1976; Mundy, 1984). The diet of *P. vetulus* larvae from 1971 was still dominated by appendicularians (Fig. 8; Table 3), indicating that these larvae are highly selective for appendicularian prey; more *P. vetulus* larvae in 1971 than in 1973 had empty guts (Fig. 4), however, and a much larger percentage of small *P. vetulus* larvae were collected in 1971 during both day and night hours, perhaps indicating decreased survival to larger sizes due to starvation (Richardson and Pearcy, 1977; Laroche and Richardson, 1979).

Given the specific prey requirements for *Parophrys vetulus* larvae, the potential exists for a match-mismatch situation where the peak of spawning may not coincide with the peak productivity of its prey, resulting in significant food-related mortality. The 'match-mismatch' hypothesis developed by Cushing (1978) states that the degree of overlap between peaks of production of larvae and their food might be positively related to the magnitude of the subsequent year-class. A major factor in the synchronization of larval fish and food source abundances is spawning time (Cushing, 1975). Kruse and Tyler (1983) have found that the timing of *P. vetulus* spawning off Oregon is primarily linked to upwelling-influenced changes in bottom

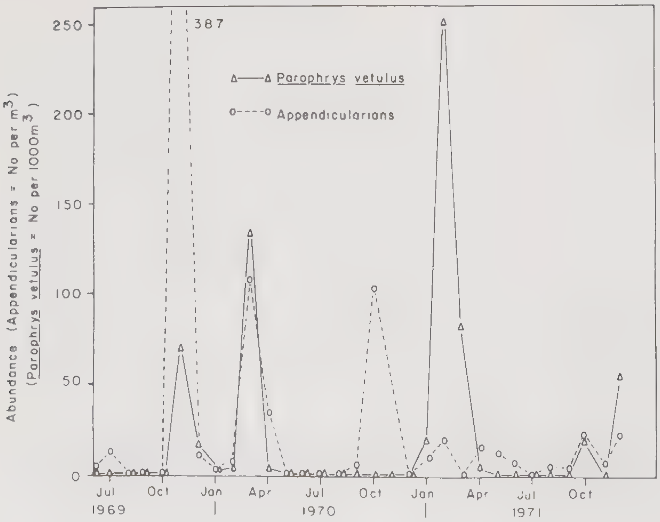

Fig. 11. *Parophrys vetulus* larvae (information from Mundy, 1984) and appendicularian mean abundances (information from Peterson and Miller, 1976) at NH5 from June 1969 through December 1971

temperatures; spawning is inhibited during upwelling. Unlike that of most temperate marine fishes, spawning of *P. vetulus* is characterized by an extended season, with spawning peaks occurring from September to March (Laroche and Richardson, 1979; Mundy, 1984). Since appendicularian abundance may also be affected by upwelling (Peterson and Miller, 1976), the same physical factors may control abundances of both larvae and their prey.

The different spawning period lengths and timings of *Isopsetta isolepis* and *Parophrys vetulus* are adapted to their feeding strategies. *I. isolepis* larvae predominantly feed on the most common and abundant zooplankters, and therefore have a greater chance that an appropriate food source will be available during their more limited pelagic larval stage. The more protracted spawning period of *P. vetulus*, often with multiple abundance peaks, enhances the probability that some larvae are present during high appendicularian abundances. Hence, factors important in determining *P. vetulus* year-class strength are those related to the timing of larvae and appendicularian abundance peaks.

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Trapping Surveys for the Deepwater Caridean Shrimps, *Heterocarpus laevigatus* and *H. ensifer*, in the Northwestern Hawaiian Islands

REGINALD M. GOODING

Introduction

The caridean shrimps, *Heterocarpus laevigatus* Bate and *H. ensifer* Milne Edwards (Fig. 1), are deepwater species with a mid-latitude circumglobal distribution extending throughout the eastern and western Atlantic, Indo-west Pacific, Hawaii, and Indian Ocean (Holthuis, 1980). *Heterocarpus laevigatus* inhabits a deeper depth range than *H. ensifer* and, because of its larger size, is generally considered to have the greater commercial potential.

Experimental trapping surveys have shown that both species are widely distributed throughout the central and western Pacific. Exploratory trap fishing has been conducted in Hawaii (Clarke, 1972; Struhsaker and Aasted, 1974); Guam (Wilder, 1977; Moffitt, 1983); New Caledonia (Intès, 1978); Fiji (Brown and King, 1979); Western Samoa (King, 1980a); Vanuatu (King, 1980b, 1981c); Tonga (King, 1981a); and Papua New Guinea (King, 1982).

The available literature indicates that in the Pacific outside of Hawaii *Heterocarpus* is commercially exploited only in a trawl fishery for *H. reedi* off

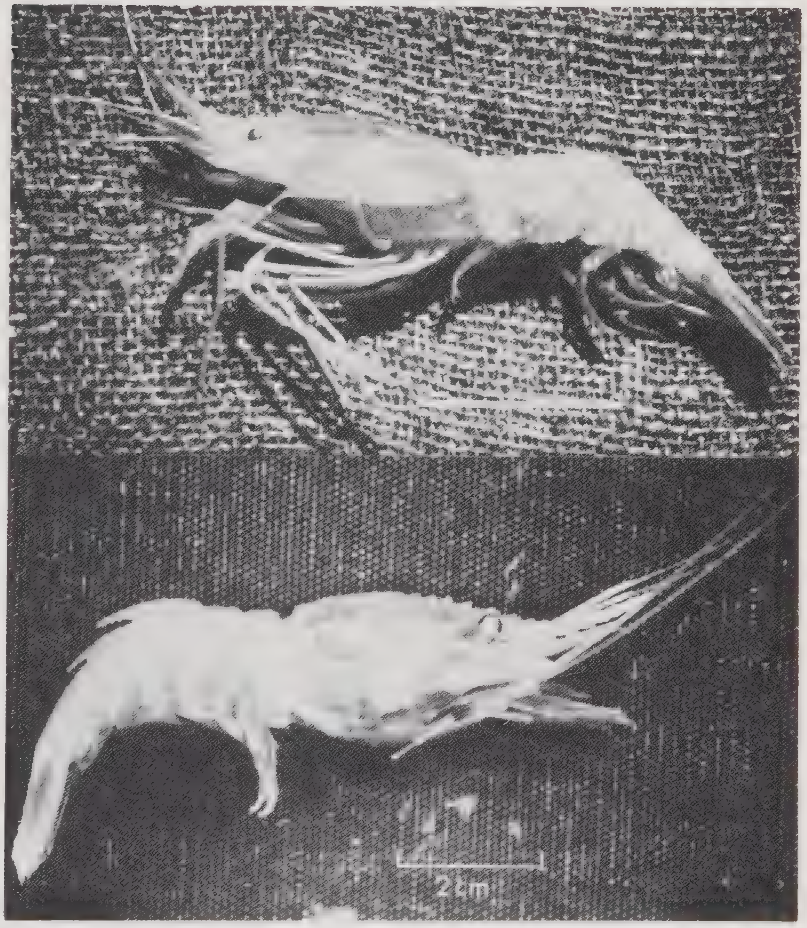

Figure 1.—*Heterocarpus ensifer* (top) and *H. laevigatus*.

ABSTRACT—Baited traps were used to assess the geographic and depth distribution of the deepwater caridean shrimps Heterocarpus laevigatus *and* H. ensifer *in the Northwestern Hawaiian Islands. Traps were set in depths ranging from about 290 to 880 m. Both species occurred throughout the length of the chain. Catch rates varied markedly with depth. Highest catches of* H. laevigatus *were made in 500-800 m with a mean catch rate of 0.91 kg per trap-night. For* H. ensifer, *optimum trapping depths were 350-600 m with a mean catch rate of 1.66 kg per trap-night.*

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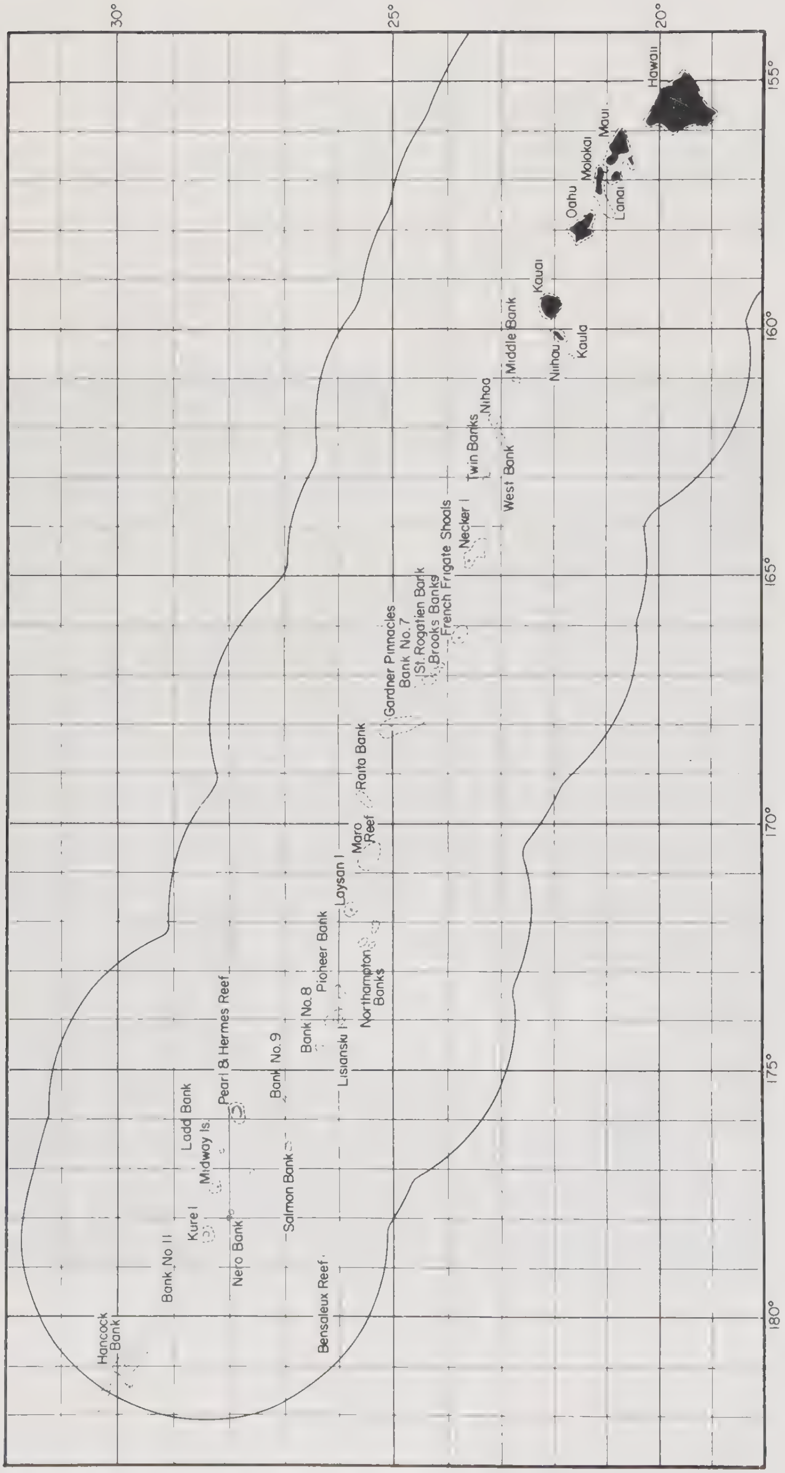
30°
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Hawaii
Maui
Molokai
Lanai
Oahu
Kauai
Niihau
Kaula
Middle Bank
Nihoa
Twin Banks
West Bank
Necker I
French Frigate Shoals
Brooks Banks
St. Rogatien Bank
Bank No.7
Gardner Pinnacles
Raita Bank
Maro Reef
Laysan I
Northampton Banks
Pioneer Bank
Bank No.8
Lisianski I
Bank No.9
Pearl & Hermes Reef
Ladd Bank
Midway Is.
Salmon Bank
Kure I
Nero Bank
Bank No.11
Bensaleux Reef
Hancock Bank

Figure 2. — The Hawaiian Archipelago including the Northwestern Hawaiian Islands.

Chile and Peru (Hancock and Henriquez, 1968; Longhurst, 1970) and in a fishery for *H. vicarius* off Costa Rica and Panama (Holthuis, 1980). Two commercial-scale projects have been conducted to determine the economic feasibility of a fishery for *H. laevigatus* and *H. ensifer* in the Hawaiian Islands (Oishi, 1983; Hawaiian Divers, Inc.[1]). At present, private interests are endeavoring to develop a fishery for deepwater shrimp in the Hawaiian Islands (Schlais, 1983).

During exploratory trawling surveys for penaeid shrimp, *Penaeus marginatus*, conducted by the Honolulu Laboratory of the National Marine Fisheries Service's (NMFS) Southwest Fisheries Center (SWFC), in 1967-68 (Yoshida, 1972), *H. ensifer* and *H. laevigatus* were caught in small numbers (Struhsaker and Yoshida, 1975). Later experimental fishing in Hawaii between 1968 and 1973 (Clarke, 1972; Struhsaker and Aasted, 1974) showed that trapping rather than trawling was a more effective method of fishing for *H. ensifer* and *H. laevigatus*. Those early surveys indicated that the two species might constitute an unexploited resource of considerable commercial potential.

In response to recommendations from the Governor's Task Force on Oceanography of the State of Hawaii (Department of Planning and Economic Development, 1969, 1974), NMFS conducted exploratory deepwater shrimp trapping in various areas in the Hawaiian chain (Struhsaker and Aasted, 1974), including Necker Island, French Frigate Shoals, Laysan Island, and Pioneer Bank in the Northwestern Hawaiian Islands (NWHI) (Fig. 2). From 1975 to 1982, in a cooperative research effort with several other agencies to investigate NWHI marine and terrestrial resources, NMFS made extensive surveys of the offshore finfish and crustacean resources throughout the NWHI

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[1] Hawaiian Divers, Inc. 1983. Deepwater shrimp utilization study for Hawaii. Report prepared under NOAA Cooperative Agreement No. 80-ABH-00065 for the Southwest Region, Western Pacific Program Office, Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812. 48 p. (On file at NMFS Southwest Fish. Cent., Honolulu, HI 96812.)

(Uchida et al., 1980). From 1978 to 1981 exploratory trapping for deep-water shrimps was conducted during nine cruises (TC-78-03, TC-79-03, TC-80-02, TC-80-03, TC-80-04, TC-80-05, TC-81-01, TC-81-02, and TC-81-04) of the NOAA ship *Townsend Cromwell*. This report is based on the data collected during that period.

Gear and Methods

The shrimp traps (Fig. 3) were half round, with a frame constructed of 1.27 cm reinforcing steel, covered with 1.27 × 2.54 cm mesh hardware cloth. At each end they had a quadrant-shaped entry of a mean width about 33 cm tapering to an inner opening 8-10 cm in diameter. A bait container (12 × 12 × 27 cm) made of the same mesh hardware cloth was located at the top of each trap near one entrance. On the basis of field tests which showed that covered traps outfished uncovered traps by factors of from 2.5 to 10 (Struhsaker and Aasted, 1974), the tops of the traps were covered with black canvas or burlap. It is generally believed that covered traps may be more effective because the bait scent tends to be concentrated at the trap entrances and cannot easily diffuse through the trap mesh, as it might in uncovered traps. No tests were made during this survey to compare covered and uncovered traps; however, King (1981c) found no significant difference in the mean catch rates of *H. ensifer* between covered and uncovered traps. The number of traps and spacing on the ground line were not consistent throughout the survey. Most sets consisted of either four or five traps spaced 36 m apart. On a few sets, however, six trap strings were fished or traps were spaced at 18 or 45 m. The traps were usually weighted with about 5 kg of chain link, and an anchor was attached to the end trap of each string.

The ground line and buoy line were 1.27 cm polypropylene rope. The buoy line was made up of 92 or 185 m lengths, which were stored in 121 l (32-gallon) plastic garbage containers. This facilitated adjustment of the length of the buoy line appropriate to the depth. To minimize the possibility of marker buoy submergence due to current drag or to trap strings slipping into deeper water, at least a 2:1 and frequently a 3:1 scope ratio was used. The markers consisted of weighted bamboo flagpoles buoyed with either large spherical inflatable or rigid plastic floats. Another plastic float at the end of a short trail line provided reserve buoyancy and facilitated gear retrieval. The bait used throughout the survey period consisted of from two to three (about 1 kg) whole fish, usually either jack mackerel or Pacific mackerel. Trapping stations were occupied from 1600 to 1800 hours in the afternoon until 0800-1000 hours the following morning, allowing an overnight soaking time of 14-18 hours.

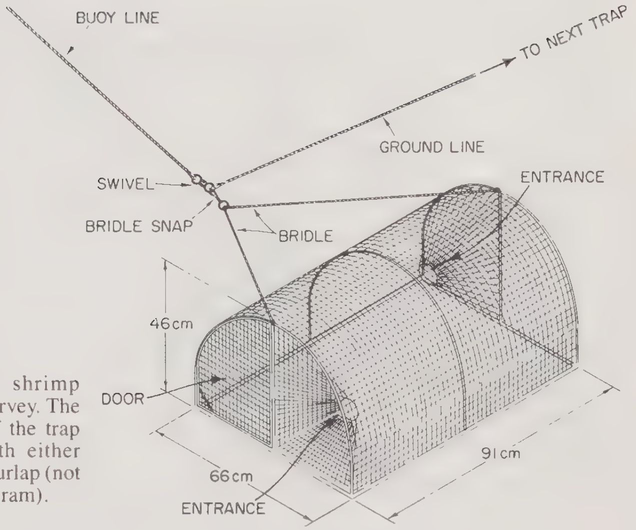

Figure 3.—The shrimp trap used in the survey. The half-round top of the trap was covered with either black canvas or burlap (not shown in the diagram).

The combination of strong currents and precipitous dropoffs along the NWHI banks frequently made it difficult to locate suitable areas for trap stations. To keep gear loss to a minimum, depth sounding transects were always made before setting to determine areas where the slope was not too steep.

Results and Discussion

Fishing Effort and Geographic Distribution

Fifty-four fishing stations consisting of 458 trap-nights of fishing effort were occupied on 17 banks along the entire length of the NWHI. Totals of 199.06 kg of *H. laevigatus* and 479.69 kg of *H. ensifer* were trapped. The fishing effort was not evenly distributed. Some banks such as Necker, French Frigate Shoals, Gardner Pinnacles, and Maro Reef were relatively well surveyed, whereas very little effort was expended on others. Table 1 shows the trapping effort, catch rates, and depth ranges for all banks sampled. Both species were taken at all of the survey areas except Brooks Banks, Raita Bank, Laysan Island, and Lisianski Island, where only *H. ensifer* were caught, and Ladd Bank, where neither species was caught. Some sets at those areas were in depths where *H. laevigatus* usually occurred in other areas sampled. Throughout the survey, however, there was considerable variation in catch rates among traps within a set, and between sets made in the same area at similar depths. Thus, on the basis of the data available, there is little reason not to assume that both species occur at appropriate depths on all the banks in the NWHI chain.

Depth Range

In this report, catch data are related to depth of capture. The distribution of shrimp is possibly related more directly to temperature; however, temperature data were not routinely collected. Depths ranging from 290 to 880 m were sampled; however, depths of <300 m and >800 m received relatively little effort. Figure 4 shows the effort and the catch per unit effort (CPUE) for 50 m depth zones for both species.

Our trapping effort clearly did not sample the shallowest depths at which

Table 1.—Fishing effort, depth range fished, total catches, and catch per unit effort for all areas surveyed in the Northwestern Hawaiian Islands.

			H. laevigatus		*H. ensifer*	
Fishing area	Effort (trap-nights)	Depth range fished (m)	Total catch (kg)	Mean catch per trap-night	Total catch (kg)	Mean catch per trap-night
Southern area						
Nihoa Island	23	368-600	1.38	0.06	25.07	1.09
West Bank	16	338-732	2.16	0.16	7.52	0.47
Twin Banks	6	468	4.44	0.74	20.28	3.38
Necker Island	88	289-867	45.76	0.52	127.60	1.45
French Frigate Shoals	53	368-733	17.49	0.33	129.85	2.45
Brooks Banks	20	329-485	0	0	11.00	0.55
St. Rogatien Bank	31	309-766	7.15	0.23	23.25	0.75
Bank No. 7	12	481-821	8.64	0.72	0.96	0.08
Northern area						
Gardner Pinnacles	70	68-758	83.30	1.19	48.30	0.69
Raita Bank	12	399-427	0	0	15.84	1.32
Maro Reef	74	287-772	25.90	0.35	48.10	0.65
Laysan Island	12	331-879	0	0	1.80	0.15
Northampton Bank	12	540-690	1.20	0.10	3.12	0.26
Lisianski Island	8	459-561	0	0	12.24	1.53
Salmon Bank	12	512-647	0.84	0.07	0.36	0.03
Ladd Bank	4	566	0	0	0	0
Kure Atoll	5	562	0.80	0.16	4.40	0.88

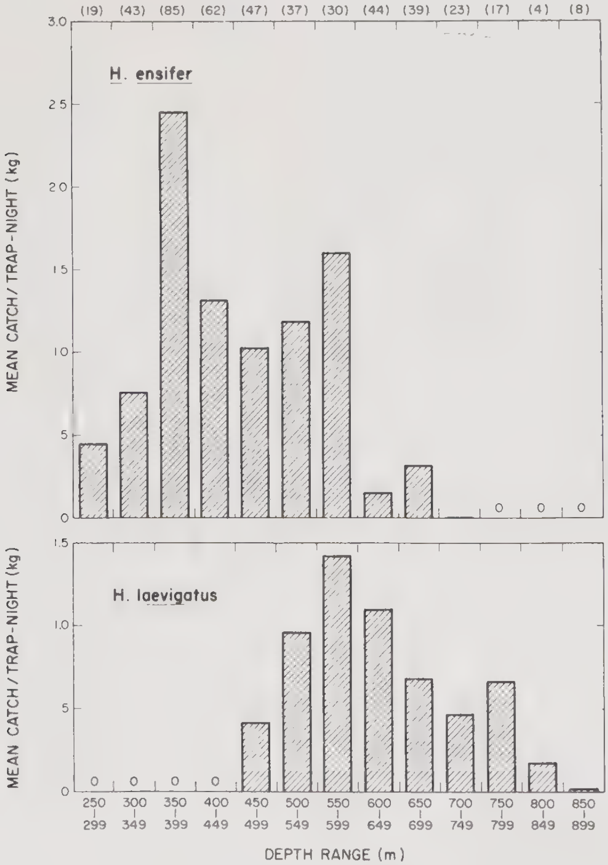

Figure 4.—Catch per trap-night of *Heterocarpus ensifer* and *H. laevigatus* per 50 m depth zone. Effort (trap-nights) is shown in parentheses.

H. ensifer probably occurs in the NWHI. In the main Hawaiian Islands, Clarke (1972) caught *H. ensifer* between 145 and 740 m, and Struhsaker and Aasted (1974) took *H. ensifer* in depths ranging from 137 to 660 m.

Heterocarpus laevigatus were trapped between 453 and 867 m (Fig. 4). Although there were small catches in the 850-899 m depth zone, it appears likely this was close to the maximum depth for this species in the NWHI. Clarke (1972) collected *H. laevigatus* from 365 to 728 m, and Struhsaker and Aasted (1974) caught them in depths from 430 to 825 m. Results obtained by investigators in other areas of the Pacific do not extend maximum depths below those we obtained. King (1981b) reported depth ranges in the southwestern Pacific islands of 285-760 m for *H. ensifer* and 380-860 m for *H. laevigatus*. In his surveys, the range of depth distribution for both species differed to some extent in the various island groups he surveyed. Wilder (1977) found *H. laevigatus* in depths ranging from 457 to 732 m off Guam, but apparently did not sample below the maximum depth he reported for the species.

Of more significance to a fishery are depths of optimum abundance. Figure 4 indicates that the approximate optimum depth range for trapping *H. ensifer* in the NWHI was 350-599 m. Struhsaker and Aasted (1974) found peak abundance of *H. ensifer* in depths of 365-440 m, and Clarke (1972) concluded they were most abundant in depths of 275-455 m. Comparison of the deep end of our optimum depth range with that found by the earlier investigations in the main Hawaiian Islands indicates, as first suggested by Struhsaker and Aasted (1974), that peak abundance of *H. ensifer* may occur deeper in the NWHI than in the main Hawaiian Islands. During exploratory shrimp trapping off the Island of Hawaii by the SWFC Honolulu Laboratory, the optimum depth range for *H. ensifer* was [2]335-618 m, a range very similar to that found during the NWHI survey.

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[2] Narrative report, *Townsend Cromwell* cruise 79-05. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.

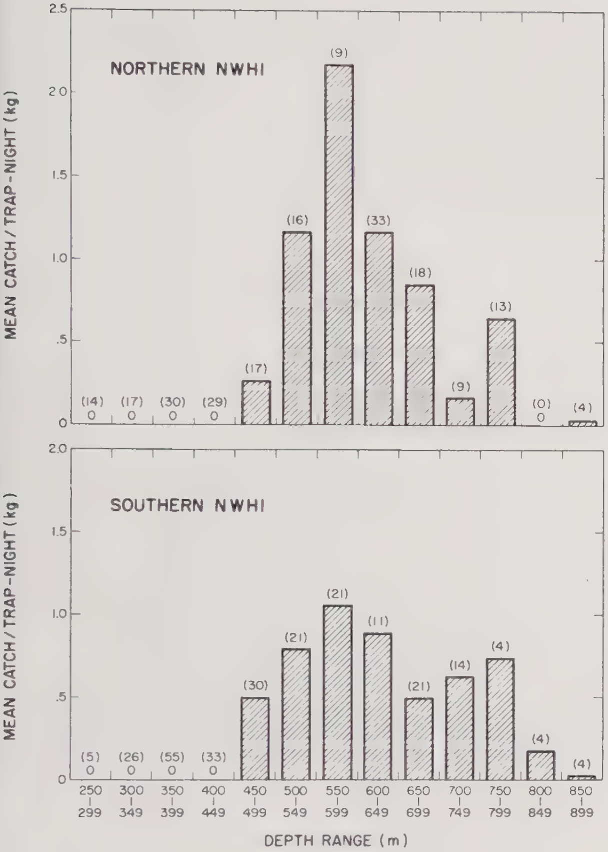

Figure 5.—Catch per trap-night of *Heterocarpus laevigatus* per 50 m depth zone for the northern and southern Northwestern Hawaiian Islands. Effort (trap-nights) is shown in parentheses.

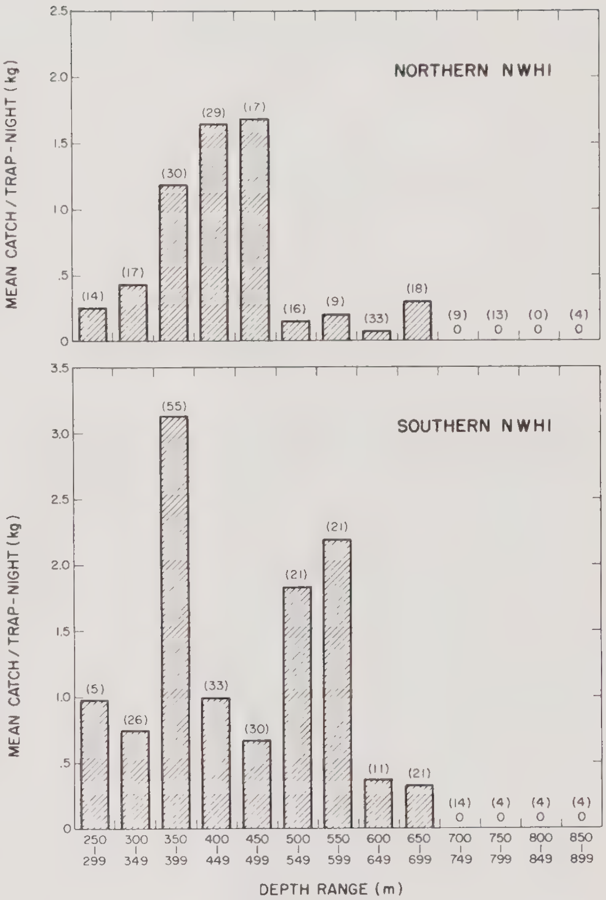

Figure 6.—Catch per trap-night of *Heterocarpus ensifer* per 50 m depth zone for the northern and southern Northwestern Hawaiian Islands. Effort (trap-nights) is shown in parentheses.

The optimum depth range for *H. laevigatus* was 500-799 m (Fig. 4), compared with a range of 440-684 m estimated by Struhsaker and Aasted (1974). The available data seem to indicate that *H. laevigatus* may occur at shallower depths in the main Hawaiian Islands than in the NWHI. During this survey, *H. laevigatus* were not caught in <453 m whereas they have been taken at 365 m (Clarke, 1972), 430 m (Struhsaker and Aasted, 1974), and 391 m (footnote 2). At Kure Atoll, the most northerly area sampled, the CPUE of *H. laevigatus* was low at a trapping depth of 562 m (Table 1) which was in the depth zone of peak catches for the overall NWHI survey. However, no other depths were sampled at Kure Atoll. Commercial fishing interests have also found that both *H. laevigatus* and *H. ensifer* occur deeper in the NWHI than in the main islands[3].

Northern and Southern Areas

The data did not allow an examination of south to north trends within the NWHI. In an attempt to determine if there were any obvious differences in catch rates and depth distribution of the two species between southern and northern sections of the survey area, the catch data were segregated for Nihoa Island to Bank No. 7 (southern area) and Gardner Pinnacles to Kure Atoll (northern area) (Fig. 5, 6). The two areas were chosen on the basis of more or less equally distributed sampling effort. A total of 249 trap-nights were fished in the southern area and 209 trap-nights in the northern area.

There was no indication that within the NWHI the peak abundance of *H.*

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[3] M. D. Dailey, Hawaiian Islands Shrimp Co., 737 Bishop Street, Suite 2910, Honolulu, HI 96813. Pers. commun., January 1984.

laevigatus occurred any deeper in the northern part of the survey area. Figure 5 shows that the depth distributions for that species were very similar in the southern and northern sections. The CPUE peaked at the 550-599 m depth zone in both areas; however, catch rates were higher for nearly all the depth zones in the north.

For *H. ensifer* in the northern area (Fig. 6), the highest catch rates were confined to depths ranging from 350 to 499 m, whereas in the south the better catches were spread across a wider range of depths (250 to 599 m). Again, for this species there is no indication that peak abundance occurred any deeper in the north. Indeed, the available data indicate the opposite.

Size by Depth

Previous investigators have demonstrated that the maximum mean size of *H. ensifer* occurs within the depth range of peak abundance, and smaller shrimp occur at shallower and deeper depths (Clarke, 1972; Struhsaker and Aasted, 1974; King, 1981c). During the NWHI survey, length data were not routinely collected. However, total number of individuals and total weight of the two species were recorded, allowing calculation of mean individual weight per trap.

For *H. ensifer*, the NWHI data are in partial agreement with those of other surveys. There was a trend toward decreasing size as depth increased from 450 m to the maximum depth (Fig. 7), which paralleled the sharply declining CPUE over the same depth range (Fig. 4). However, at the depth of peak abundance (350-399 m), there was actually a decline in mean individual weight and an increase towards the shallowest depth sampled. It is possible that had shallower depths been sampled, there may have been a decline in shrimp weight towards the shallowest end of the depth range.

As with *H. ensifer*, the NWHI data for *H. laevigatus* indicate a decline in shrimp size only from the depth range of peak abundance towards deeper water. Figures 4 and 7 show that relatively large *H. laevigatus* were caught at the shallowest end of their range, and that the largest weight class occurred at the depth zone of maximum abundance (550-599 m). Net mean individual weight declined with CPUE towards the deep end of the range.

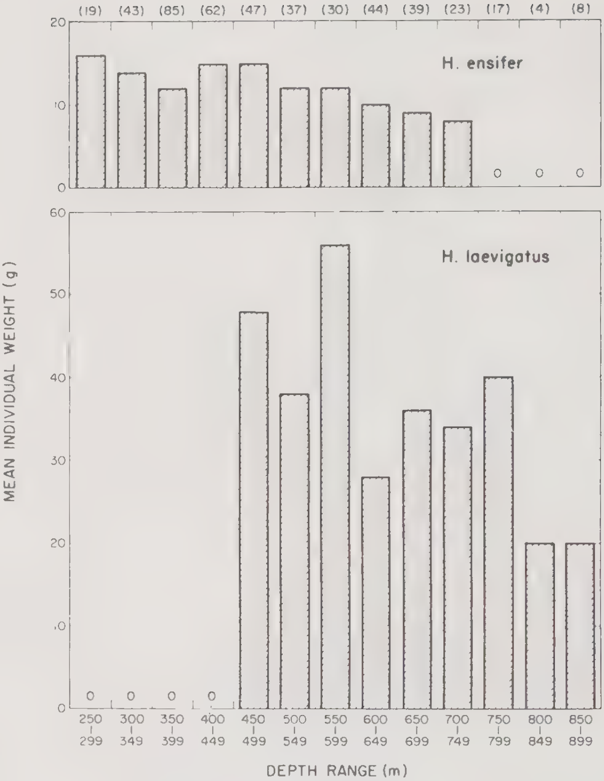

Figure 7.—Mean individual weight of *Heterocarpus ensifer* and *H. laevigatus* per 50 m depth zone. Effort (trap-nights) is shown in parentheses.

The relationship between CPUE (in terms of weight) and depth was not significantly affected by variations in mean weight of the shrimp. Figure 8 shows numbers of shrimp per trap-night per depth zone. The only marked change in the overall picture when the data are presented this way is that for *H. laevigatus* there was a shift in peak abundance from the 550-599 m to the 600-649 m depth zone, further emphasizing the sharp decline in the weight of *H. laevigatus* between the two zones (Fig. 7).

Catch by Season

Clarke (1972) did not get a clear picture of seasonal change, based on data from single trap sets off Kaneohe, Oahu, at 1-month intervals from January to October. His very limited data indicated that all low catches and no really large ones were made between March and September, suggesting lower abundance during the summer. In Fiji, King (In press) found that catch rates did not change significantly with season.

During the NWHI survey, the trapping effort was not well distributed over all months or even seasons. The midsummer months received a large proportion of the effort whereas the midwinter months received relatively little effort. However, when the data are segregated on a two-season basis, the distribution of effort is reasonably good (273 trap-nights during April-September, and 185 trap-nights during October-March). Figure 9 shows the CPUE and mean

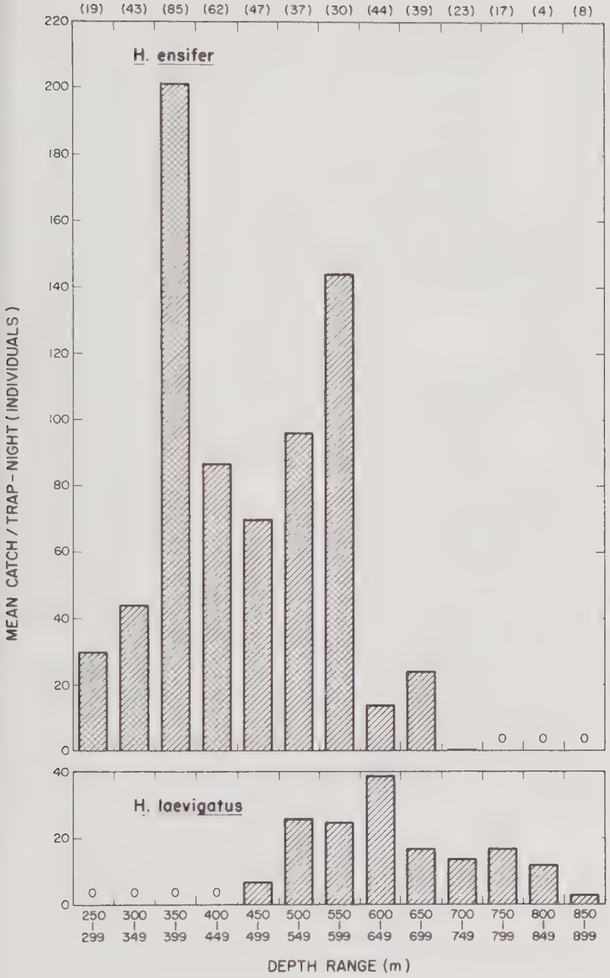

Figure 8.—Mean catch per trap-night (individuals) per 50 m depth zone. Effort (trap-nights) is shown in parentheses.

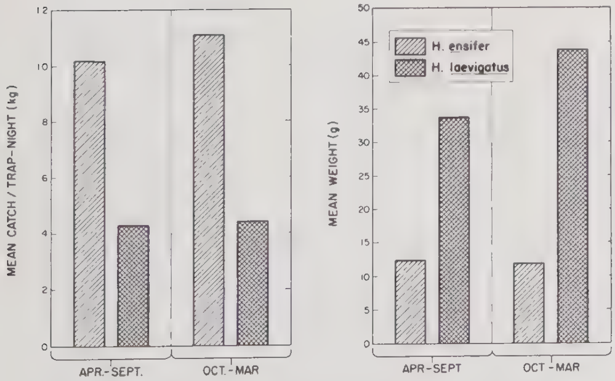

Figure 9.—Mean catch per trap-night and mean individual weight of *Heterocarpus ensifer* and *H. laevigatus* for spring-summer and fall-winter seasons.

weight of catch for spring-summer and fall-winter seasons. The CPUE for both species of *Heterocarpus* was almost identical for both periods. There was no difference in the mean weight of the catch of *H. ensifer* taken in April-September, compared with October-March. The mean weight of *H. laevigatus* was larger in the October-March catches than in the April-September catches. Figures 10 and 11 show the mean catch rate of each species per 50 m depth zones for spring-summer and fall-winter periods. It is interesting that the high catch rates of *H. laevigatus* in depths of 550-599 m were experienced only during the October-March period. Otherwise, there is no indication that the depth range of optimum abundance for either species differed significantly between the two seasons.

Comparison With Commercial Shrimp Trapping

As part of a study to define the distribution and magnitude of *Heterocarpus* resources in the Hawaiian Islands, in 1981 two commercial fishing vessels were chartered to conduct shrimp trapping at Maro Reef (Oishi, 1983). They set a total of 9,914 traps, and had a mean catch rate of 2.47 kg of both species per trap-night. It is of interest to compare such a relatively intense effort on a commercial scale with results obtained during this survey at the four areas most intensely sampled: Necker, French Frigate Shoals, Gardner Pinnacles, and Maro Reef. The catch rates given in Table 2 are based only on trap sets made at optimum depth ranges for each

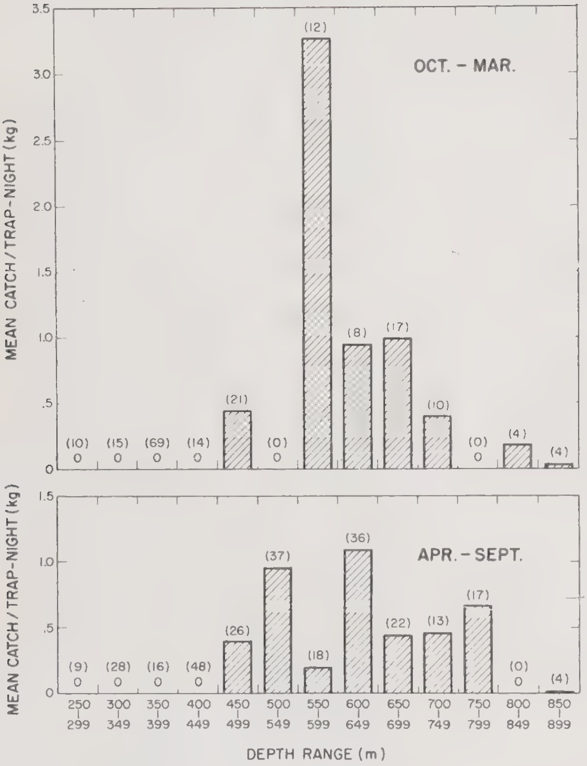

Figure 10.—Catch per trap-night of *Heterocarpus laevigatus* per 50 m depth zone for spring-summer and fall-winter seasons. Effort (trap-nights) is shown in parentheses.

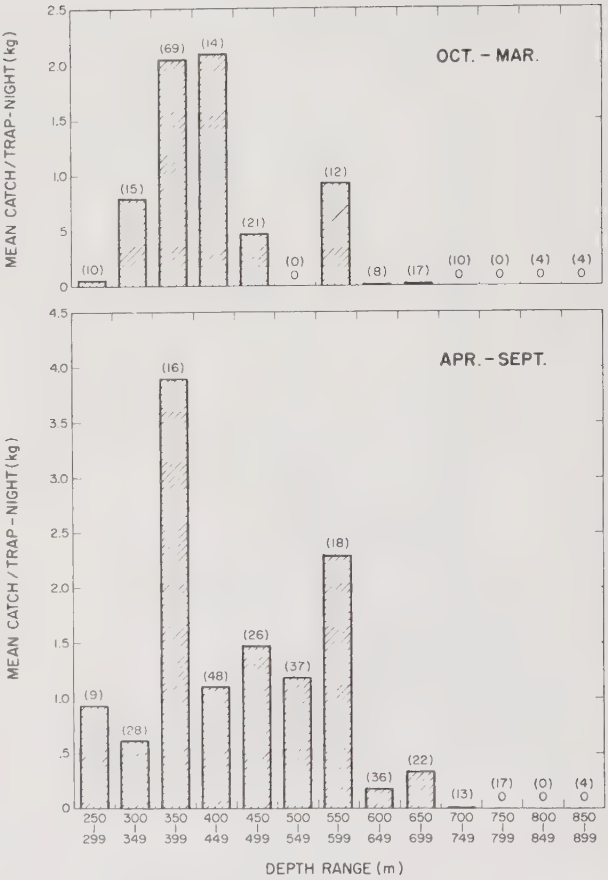

Figure 11.—Catch per trap-night of *Heterocarpus ensifer* per 50 m depth zone for spring-summer and fall-winter seasons. Effort (trap-nights) is shown in parentheses.

Table 2.—Mean catch per trap-night (kg) at optimum depth range[1].

Area	*H. ensifer*	*H. laevigatus*	Both species
Necker Island	1.65	1.18	2.83
Fr. Frigate Shoals	3.77	0.37	4.14
Gardner Pinnacles	1.17	2.09	3.26
Maro Reef	1.16	0.97	2.13

[1] 350-599 m for *H. ensifer*; 500-799 m for *H. laevigatus*

species. Highest total CPUE was obtained at French Frigate Shoals where the total mean catch as 4.14 kg per trap-night. At French Frigate Shoals 75 percent of the trapping effort was within the optimum depth range for *H. laevigatus*. Despite this, catch rates for that species were very low. The catch rate at Maro Reef was the lowest for the four fishing areas. However, the CPUE of 2.13 kg at Maro Reef was quite similar to the CPUE of 2.47 during the commercial survey in the same area. Private interests are presently conducting extensive commercial trapping for *H. laevigatus* in the NWHI. No information from these operations was available at the time of writing.

Summary

During exploratory fishing operations for the deepwater caridean shrimps *H. laevigatus* and *H. ensifer* from 1978 to 1981, both species were trapped throughout the NWHI. Based on catch rates, peak abundance occurred at depths between 500 and 799 m for *H. laevigatus* and 350 and 599 m for *H. ensifer*. For both species there was an apparent decline in size as the depth range increased from that of peak abundance to maximum depth. There was no evidence that for either species the depth range differed significantly between the northern and southern banks of the chain, or between spring-summer and fall-winter seasons.

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Close genetic similarity of Atlantic and Pacific skipjack tuna (*Katsuwonus pelamis*) demonstrated with restriction endonuclease analysis of mitochondrial DNA

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Abstract

Restriction endonuclease analysis of mitochondrial DNA indicated a surprisingly high degree of genetic similarity between skipjack tuna (*Katsuwonus pelamis*) from the Atlantic and Pacific Oceans. The present results (1983) support the findings of previous morphological and electrophoretic studies. Evidently, since the uplift of the Panamá land bridge about 3.1 million years ago, there has been continued genetic contact between Atlantic and Pacific skipjack tuna, presumably via the Southern Ocean.

Introduction

Effective fishery management requires an understanding of the population or stock structure of the exploited organism. To investigate the genetic basis of stock structure, one must study genetic characters that demonstrate sufficient variation to permit discrimination of intraspecific groups or stocks. The genetic basis of population structure of skipjack tuna (*Katsuwonus pelamis*) has been reviewed by Argue (1981). From studies of meristic, morphometric and electrophoretic characters of skipjack tuna, geneticists have detected little character variation and have demonstrated only slight differentiation between individuals from different ocean basins. The apparent lack of significant differentiation in genetic characters could either be attributed to strong selection resulting in the conservation of the analyzed characters, or sufficient gene flow among ocean basins to prevent differentiation. To distinguish between the alternatives of character conservation or gene flow is difficult, since one must search for additional characters with enough intraspecific variation to detect differentiation if it exists, or ultimately accept the null hypothesis of gene flow.

Recent studies have reported high levels of inter- and intraspecific variation of mitochondrial DNA (mtDNA) sequences of several organisms (reviewed by Avise and Lansman, 1983). It appears that mtDNA evolves about an order of magnitude more rapidly than single-copy nuclear DNA (Brown *et al.*, 1982). Fragment pattern analyses of mtDNA from several mammalian species have shown that individuals from the same population typically possess very similar mtDNA sequences, while individuals from different populations exhibit some mtDNA sequence divergence (Avise and Lansman, 1983). Consequently, mtDNA sequence differences between populations can be determined with small sample sizes. Sequence differentiation of mtDNA becomes more pronounced at the subspecies and species level (Brown, 1983). The optimal resolution of mtDNA sequence differences occur for populations that have been separated for 0.25 to 5 million years (Brown *et al.*, 1982).

Unlike nuclear DNA, mtDNA appears to be maternally inherited and does not undergo recombination during meiosis in metazoans (Giles *et al.*, 1980). It exists as a closed circular molecule of 15 000 to 18 000 nucleotide base pairs which encode two ribosomal RNAs, 22 transfer RNAs and 13 messenger RNAs (reviewed by Brown, 1983). The complete nucleotide sequences of mouse, cow and human mtDNAs have recently been published (Anderson *et al.*, 1981, 1982; Bibb *et al.*, 1981). These and other sequence studies have demonstrated that while both the function and order of the mitochondrial genome are highly conserved in vertebrates, there appears to be considerable inter- and intraspecific variation of the nucleotide sequence.

Sequencing the mitochondrial genome is a costly and time-consuming process which is currently not practical for population studies. However, the sequence of the mitochondrial genome can be sampled with restriction endonucleases, enzymes which recognize specific 4, 5 or 6 nucleotide base pairs and consistently break the DNA within the recognition site. Nucleotide substitutions in the 4, 5 or 6 base-pair recognition site prevent endonuclease cleavage and thus reduce the number of mtDNA fragments. Similarly, base-pair substitutions outside the recognition site may create a new cleavage site and mtDNA fragment. After digestion with a restriction enzyme, mtDNA fragments are separated by size electrophoretically and the fragment patterns of individual mtDNAs digested with the same restriction enzyme are compared. The loss or gain of a fragment (cleavage site) is assumed to result from the substitution of a single base-pair. Typically, several different restriction endonucleases are used in a population analysis, and, from the fragment patterns, one calculates a minimum percentage mtDNA sequence divergence between individuals by established methods (Lansman *et al.*, 1981; Nei and Tajima, 1981).

Significant intraspecific variation of mtDNA sequences has been reported for several organisms and has permitted high-resolution investigations of the genetic basis of population structure (see Avise and Lansman, 1983). Studies that have compared results from (1) starch-gel electrophoresis of water-soluble proteins, and (2) from mtDNA restriction endonuclease analysis have demonstrated that the latter technique uncovers considerably more intraspecific variation and differentiation (Lansman *et al.*, 1983). Furthermore, because of the faster rate of mtDNA evolution, population-specific differences in mtDNA sequences accumulate more rapidly than electrophoretic differences, and significant genetic differentiation can be observed with smaller sample sizes (Lansman *et al.*, 1983).

The purpose of the present study was to examine the amount of variation in mtDNA sequence both within and between samples of Atlantic and Pacific skipjack tuna (*Katsuwonus pelamis*). This paper, which is the first study of intraspecific mtDNA variation in fishes, presents evidence of possible gene flow between skipjack tuna from the Atlantic and Pacific Oceans.

Materials and methods

Freshly caught and iced skipjack tuna (*Katsuwonus pelamis*) were purchased from fish markets in Honolulu, Hawaii ($n=9$) and Rio de Janeiro, Brazil ($n=6$), and a single specimen was purchased in Ponce, Puerto Rico. Livers and hearts were removed from the fish shortly after purchase and immediately frozen on dry ice. All samples were shipped on dry ice to the laboratory, where they were stored at −70 °C until processing. The study was performed in 1983.

Protocols for the purification and analysis of mtDNA used in this study are presented in Brown *et al.* (1979) and Lansman *et al.* (1981). Because yields of purified skipjack mtDNA from frozen tissue were low, it was necessary to endlabel mtDNA fragments with radioactive nucleotide triphosphates after restriction endonuclease digestion in order to visualize band patterns after electrophoresis (described by Lansman *et al.*, 1981). Three of the 9 Hawaiian skipjack (pooled to obtain sufficient purified mtDNA) and the single Puerto Rican skipjack were analyzed by this method.

Purification of mtDNA from contaminant nuclear DNA by density-gradient ultracentrifugation is possible only if the mtDNA remains in the denser, closed circular form. The low yields of mtDNA purified from the frozen skipjack tissues indicated that, due to freezing or handling, a large fraction of the mtDNA was not in the closed circular form. Consequently, a different method of analyzing mtDNA fragment patterns was followed for the 6 Brazilian and remaining 6 Hawaiian skipjack. For these specimens, total cellular DNA (mtDNA + nuclear DNA) was isolated, digested with restriction endonucleases, subjected to electrophoreses, and transferred to nitrocellulose filters [Southern (1975) method described by Lansman *et al.* (1981)]. Fragments of mtDNA were visualized against a background of nuclear fragments by hybridizing radioactively-labelled mtDNA purified from freshly sacrificed rainbow trout (*Salmo gairdneri*) to the skipjack mtDNA fragments. As only those fragments with high-sequence similarity will hybridize, association of labeled rainbow trout mtDNA with skipjack nuclear DNA fragments did not occur. Rainbow trout was chosen for a hybridization probe on the basis of availability. Hybridized fragment patterns were visualized autoradiographically.

The restriction endonucleases (Table 1) were purchased from New England Biochemicals and were used according to the manufacturer's directions.

Results and discussion

The 9 restriction endonucleases used in the endlabeling analysis of the mtDNA purified from the 3 pooled specimens of *Katsuwonus pelamis* from Hawaii and the single Puerto Rican specimen (Table 1) produced 25 and 26 fragments, respectively. Fragment patterns of 5 of the 9 restriction enzymes used in the endlabeling analysis were investigated in more detail in the southern (hybridization) analysis of the Brazilian and Hawaiian skipjack tuna. These 5 enzymes produced fragment patterns similar to those produced in the endlabeling analysis, and resolved an additional 14 fragments.

The size of the skipjack tuna mtDNA molecule (genome) was estimated by summing the mtDNA fragment sizes produced by a single restriction endonuclease. Fragment sizes of mtDNA were determined by comparison with the electrophoretic mobility of DNA fragments of known size (restriction enzyme digests of phage lambda DNA). The mean size of the skipjack tuna mtDNA genome, calculated from several digests with 5 restriction enzymes (*Hind* III, *Pst* I, *Sac* I, *Pvu* II and *Ava* II), was 16 900 base pairs for fish from both oceans. This value agrees well with the size of 16 700 base pairs reported for the mtDNA of 4 species of salmonids (Berg and Ferris, 1984) and is about 400 base pairs greater than the value reported for humans (Brown, 1981).

The number of base pairs examined in this study can be determined precisely. With the southern method, the

Table 1. Restriction endonucleases employed, number of base pairs recognized at the restriction (cleavage) site, and resultant patterns observed in the skipjack tuna *Katsuwonus pelamis*. Two types of analyses were performed: (a) mtDNA was purified and fragments were endlabeled with radioactive deoxynucleotide triphosphates to enhance visualization on the gel; (b) Southern transfers of total genomic DNA were hybridized with a probe made from salmon (*Salmo gairdneri*) mtDNA (see Ferris *et al.*, 1981). HI = Hawaiian, PR = Puerto Rican, and BRZ = Brazilian samples; numbers of individuals tested are given in parentheses; w = "wild" type (common pattern), var = "variant" type (mutated pattern). Dash = not examined

Enzyme type	Recognition sites (base pairs)	Restriction patterns			
		Endlabeled		Southern method	
		HI (3 pooled)	PR (1)	HI (6)	BRZ (6)
Hind III	6	w	w	–	–
Hpa II	4	w	w	w	w
Mbo I	4	w	w	–	–
Pst I	6	w	var	w	w
Eco RI	6	w	w	–	–
Xba I	6	w	w	–	–
Sac I	6	w, var	–	w	w
Pvu II	6	w	–	w	w, var
Ava II	5	w, var	–	w	w

Table 2. Qualitative comparison of mtDNA variation in skipjack tunas (*Katsuwonus pelamis*) and in common chimpanzees (*Pan troglodytes*)

Tuna ($n = 16$)		Chimps ($n = 10$)[a]	
Enzyme type	No. of morphs	Enzyme type	No. of morphs
Hpa II	1	*Hpa* II	5
Pst I	2	*Pst* I	1
Sac I	2	*Sac* I	2
Pvu II	2	*Pvu* II	2
Ava II	2	*Ava* II	3
Total	9		13

[a] From Ferris *et al.* (1981)

restriction enzymes *Pst* I, *Sac* I and *Pvu* II, which recognize 6 base-pair sites (Table 1), made 2, 2 and 3 restrictions respectively, while *Ava* II which recognizes 5 base pairs, made 3 cleavages and *Hpa* II, a restriction enzyme which recognizes 4 base pairs, created 4 detectable fragments. Thus, a total of 73 base pairs was surveyed by the southern method. The restriction endonucleases used in the endlabeling method recognized an additional 96 base-pairs for a grand total of 169 base-pairs, about 1% of the total skipjack mtDNA genome.

Intraspecific variation in fragment patterns, reflecting variation in mtDNA nucleotide sequences, was demonstrated with 4 of the 9 restriction enzymes (Table 1). However, none of the fragments demonstrated consistent differences between fish from the two oceans. Three fragments were different between the Hawaiian skipjack tuna and the Puerto Rican specimen investigated in the endlabeling analysis, attributable to a single *Pst* I mutation in the Puerto Rican fish mtDNA. The other Atlantic skipjack tuna from Brazil had *Pst* I digestion patterns similar to those of the Hawaiian fish, and thus the Puerto Rican skipjack appears to be variant. Within-ocean variants were also found for digests with *Sac* I, *Pvu* II and *Ava* II (Table 1).

Currently there are no available data on intraspecific sequence variation in fishes with which to compare the results of this study. However, they can be compared with mammalian data obtained with the same restriction enzymes. Table 2 presents the mtDNA variation in common chimpanzees (*Pan troglodytes*) which is typical of other mammals (Ferris *et al.*, 1981). The chimpanzees exhibited 13 morphs for 10 individuals tested, whereas for the skipjack tuna only 9 morphs were discovered in 16 individuals examined. Thus, intraspecific mtDNA sequence variation in the skipjack tuna was less than in most mammals, although higher than levels reported for some mammals (Avise and Lansman, 1983); the variation in the tuna certainly appears sufficiently high to reveal significant intraspecific differentiation if it indeed exists.

The present study represents a limited investigation of mtDNA variation within and between Atlantic and Pacific skipjack tuna. The total number of base-pairs examined and the number of base-pairs examined per individual in this study are low compared with some recent mammalian studies. Furthermore, restriction enzymes which recognize 6 base-pairs were preferentially used in this study because they produce larger, more easily visualized fragments although they do not reveal as much variation as those which recognize 4 base-pairs. Even though a more extensive study of skipjack tuna will probably reveal more variants than did the present study (and perhaps even some population- or ocean-specific fragments), it is clear from these results that there is a striking lack of mtDNA differentiation between Atlantic and Pacific skipjack tuna.

Our results from a total sample of 7 Atlantic and 9 Pacific skipjack tuna demonstrate a sequence divergence of 0.0% between fish from the two oceans. Even if a restriction site had been found in fish from one ocean but not from the other, the difference would be only 1 substitution per 169 base-pairs or a sequence divergence of 0.6%. This value is very small compared to some mammalian disjunct conspecific populations which differ by about 3% (Avise and Lansman, 1983). If skipjack tuna from the Atlantic and Pacific Oceans have been separated since the uplift of the Panamá land bridge 3.1 million years ago (Keigwin, 1982) and their rate of mtDNA evolution is similar to other vertebrates studied, one would expect a sequence divergence of approximately 3% (Brown, 1983). Furthermore, this sequence divergence would be evident in each specimen sampled, and a sample size of $n = 1$ would be sufficient to demonstrate that a sequence difference existed.

Electrophoretic and immunogenetic studies of skipjack tuna have also reported a high degree of genetic similarity between fish from the Atlantic and Pacific Oceans (Fujino and Kang, 1968; Fujino, 1970; Sharp and Pirages, 1978, Fujino *et al.*, 1981). Although some of these studies report small allele frequency differences at one or two loci between fish from the two oceans, no single character has been found which can distinguish an Atlantic from a Pacific skipjack tuna. This is in contrast to the large amount of genetic differentiation reported between conspecific and closely related (geminate) pairs of tropical marine shorefishes on either side of the Panamá land bridge which are genetically distinguishable at several different electrophoretic loci per pair (Vawter *et al.*, 1980). It is interesting to note that the dolphin fish *Coryphaena hippurus*, a strictly pelagic species, is similar to the skipjack tuna in that it demonstrates no significant interocean electrophoretic differentiation (R. Rosenblatt and R. Waples, personal communication).

The high degree of genetic similarity among individual skipjack tuna and among individual dolphin fish from the two oceans suggests that there is, or recently was, genetic contact between Atlantic and Pacific populations of these pelagic species. The most plausible route for genetic interchange is around the Cape of Good Hope. A seasonal coastal sport-fishery exists for skipjack tuna in South Africa, and Japanese longline data indicate that skipjack tuna have been caught off the Cape (Silas and Pillai, 1982). Seasonal isotherm patterns are consistent with the idea that skipjack tuna and other subtropical pelagic fishes can migrate around the Cape of Good Hope (Davies, 1963). Skipjack are strong swimmers and, although definite migrations have not been demonstrated, many tagged skipjack have been recovered thousands of kilometers from the site of first capture (reviewed by Argue, 1981). As skipjack often travel in large schools, the potential exists for significant gene flow around the Cape of Good Hope.

Genetic differentiation is promoted by reproductive isolation, a physical separation of populations, and a lack of migration between populations. Skipjack tuna do not have discrete spawning areas and larvae are found circumtropically in pelagic waters (Sund *et al.*, 1981). Furthermore, seasonal isotherm data and individual tag-return records indicate that skipjack tuna have the potential to migrate between ocean basins. Although it cannot be stated with any certainty just how much migration between ocean basins occurs, or has occurred in recent times, it would appear from the results of this study that there has been sufficient interchange to prevent genetic differentiation.

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Model of a Coral Reef Ecosystem

III. Resource Limitation, Community Regulation, Fisheries Yield and Resource Management

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Abstract. The results of modelling of a coral reef ecosystem at French Frigate Shoals and independent field measures of benthic primary productivity indicate relatively good agreement between food required by consumer trophic levels and organic carbon produced by primary producers. Based upon the high internal predation necessary for the model to match primary production estimates, we reason that the ecosystem is primarily regulated from the top down by forces of predation and that primary production appears to be controlled by nutrients, rate limits, and the distribution of space and habitat. In spite of relatively high primary productivity, potential yield at the top of the food chain is low because of high internal predation and high trophic complexity (6 trophic levels). Fishery yield might be maximized by harvesting low on the food chain particularly if top carnivores can be cropped to release predator pressure on selected prey. Agreement between field measures of metabolism and model (ECOPATH) results provides reasonable confidence that the model can be used as one tool for resource management.

Introduction

One of the most important problems facing coral reef biology today is the question of what factor(s) control the production of organic carbon at all levels within the ecosystem. Are coral reefs truly nutrient limited ecosystems? Does primary production depend on the supply of nutrients (concentration or flux) across the reef? Or is primary, secondary and higher level production simply regulated by predators operating downward from the top of the food chain? And, given nutrient limitation or predator regulation or some combination of the two, what is the quantitative effect of space (available sustratum) and habitat on primary or secondary levels of benthic production? In the sense of Hairston et al. (1960) is the reef green or is it brown? That is, is production of organic matter limited by "nutrients" (Nitrate, $NH_3 \cdot PO_4^{=}$ and sunlight) from below, or by predation by grazing herbivores from above? At higher levels in the ecosystem, is production limited by the flow of nutrients up the chain or is the system controlled (regulated?) by various forces of mortality? The results of this research at French Frigate Shoals, Hawaii, the first attempt to analyze the trophic energetics of an entire atoll ecosystem, may shed some light on this major problem in coral reef biology. The approach has been to dissect a reef ecosystem or foodweb simultaneously from the bottom up and the top down. The analysis is intended to produce an understanding of the dynamics of a coral reef ecosystem out of which certain management options might logically follow.

Results of Part I and Part II

Before addressing these questions directly, it is useful to reconsider the major conclusions presented in Parts I and II of this paper (Polovina 1984; Aktinson and Grigg 1984). These are briefly restated below.

Part I

1. The average rate of net primary production for the reef ecosystem at French Frigate Shoals (adjusted to 700 km^2) predicted by the ECOPATH model is 4.3×10^6 kg/km^2/year (wet weight).

2. Net primary productivity by the plankton over the reef is about 1/10 the benthic net primary productivity.

3. The ECOPATH model estimate of net community benthic production is 2.2×10^5 kg/km^2/year.

4. The model predicts that only about 5% of the net benthic primary productivity is passed up the food chain to non-benthic reef consumers.

5. The model analysis suggests that the reef ecosystem at French Frigate Shoals consists of six trophic levels. The average ecological efficiency of all trophic levels is 0.17.

6. High internal predation exists within the heterotrophic benthos and reef fish compartments of the ecosystem.

Part II

1. Rates of metabolism and calcification of reef ecosystems (reef flats, coral knolls and lagoons) at French Frigate Shoals are similar to rates for corresponding coral reef ecosystems elsewhere in the world.

2. The average rate of net primary productivity for the reef ecosystem at French Frigate Shoals based on field measures and literature P/R ratios averaged over a year is 6.1×10^6 kg/km^2/year. The field estimate for net community production was 9.4×10^5 kg/km^2/year.

3. The P/R ratio for the entire benthic ecosystem at French Frigate Shoals was 1.10. Field results indicate that about 10% of the net primary production (6% of the gross primary production) might be permanently lost to the atoll ecosystem by burial or offshore transport.

4. The close agreement between the field and model estimates of net benthic primary productivity is interpreted as conceptual support for the ecosystem model and suggests that it can be used as a tool for resource management.

Field Validation of the Model

The model estimate of net benthic primary productivity is only slightly lower than the estimate based primarily on field measures (4.3×10^6 kg/km^2/year versus 6.1×10^6 kg/km^2/year). Given the errors associated with the calculation of each of these estimates, their agreement is closer than expected. The difference might have been even smaller were it not for high values of lagoon net productivity. The average value of net productivity for the whole system may therefore be slightly less than that calculated.

Looking at the other side of the comparison, the model estimates of net primary productivity could be too low if for example the biomass of major top carnivores at French Frigate Shoals had been initially underestimated. Also the model estimate of net primary productivity would be too low if more trophic complexity actually exists than that built into the model. On these two points, however, it is believed that neither biomass or trophic complexity were mis-approximated. Another consideration is the amount or organic carbon that might be lost to the system. Since the model estimate is based on only carbon (wet weight) flowing through the system, it cannot take into account any losses even if they exist. In Part II of this paper, it was estimated that approximately 10% of the net benthic primary productivity might be permanently lost to the system. Therefore the model estimate of NPP could be low by approximately this amount.

Returning to the field estimate, if the value of net benthic primary production is increased or lowered by 50% (the error of estimate associated with all field measures), the revised field estimate for the average net primary production of the atoll would be about 3.0–9.0×10^6 kg/km^2/year. Given either change the field estimate of net benthic primary production is still within a factor of about 2.0 of the model estimate. Hence the degree of agreement observed between these two independent estimates of net benthic primary productivity appears to be good. Similarly the field estimate of net benthic community productivity is in reasonable close agreement with the model estimate (9.4×20.5 kg/km^2/year versus 2.2×10^5 kg/km^2/year).

Coral Reef Ecosystem Dynamics

Having reviewed the results of Parts I and II of this paper and reconsidered the degrees of agreement between field and model estimates of net benthic primary productivity, it is now possible to deal with the question of community function. Are coral reef ecosystems nutrient limited or predator controlled? The results of this research as discussed below suggest that nutrient limitation is of less significance than formerly believed and that predation mortality is the most important factor controlling secondary and higher production. The balance of this section is given to a consideration of the evidence for this conclusion both from this research and the literature.

The role of predation in the ecosystem can be examined by considering ecotrophic efficiency. Ecotrophic efficiency is the fraction of a species' annual production which is consumed by predation (Ricker 1969). Based on the model's estimate of trophic efficiency of 0.17, annual production at the top level of 462 kg/km^2/year, and six trophic levels, the net benthic primary production required to support the ecosystem can be calculated as a function of ecotrophic efficiency (see Part I). For an ecotrophic efficiency of 0.95 which implies that 95% of the production of each species group is consumed by predators, the net benthic primary production required by the ecosystem is 4.2×10^6 kg/km^2/year (Table 5, Part I). The net benthic primary production estimated as a function of ecotrophic efficiency increases as ecotrophic efficiency decreases (Table 5, Part I). If as discussed earlier, our confidence interval for the net benthic primary production is from 3.0×10^6 kg/km^2/year to 9.0×10^6 kg/km^2/year, then based on Table 5, Part I, the average ecotrophic efficiency for the ecosystem at French Frigate Shoals would be contained in the interval of 0.85–1.0 which indicates that at least 85% of the production of each species group is consumed by predators. Ricker's estimates for ecotrophic efficiency for marine communities in general are somewhat lower with an estimate of 0.66 for primary consumers and 0.75 for all higher consumers (Ricker 1969). Based on the simulation presented in Table 5, Part I, and our confidence in the field estimate of net benthic primary production, it appears very likely that on the average, ecotrophic efficicency for the coral ecosystem at French Frigate Shoals exceeds 0.85. It most certainly exceeds 0.50. For example, if the ecotrophic efficiency were 0.50, the net benthic primary production required to support the ecosystem would be 104.1×10^6 kg/km^2/year or about 25 times the estimated field value (Table 5, Part I). Hence, it appears that a high level of predation mortality exists within the coral reef ecosystem at French Frigate Shoals suggesting that predation mortality is the major driving force regulating higher trophic production of the ecosystem. This model result is supported by the quantitative fit between the model and field measures of net primary and community benthic productivity.

It is now useful to distinguish between regulation of production vis-a-vis production per se. Production per se is the process of producing new organic carbon while regulation is the process that determines how much of that carbon reaches various trophic levels. Given all of the above, it is now possible to re-examine the basic question, to what extent do nutrients limit the productivity of coral reef ecosystems.

The only true test of the nutrient limitation hypothesis for a coral reef community that has been done to date, is the work of Kinsey and Domm (1974) at One Tree Island on the Great Barrier Reef where they conducted fertilization experiments over an eight month period using a lagoon patch reef system. Levels of phosphorus and nitrogen were increased by 10 and 40 fold respectively during 3 h incubations. The result showed that the rate of community primary production increased by about 50% over the previous year (Kinsey and Davies 1979). Since levels of nutrient enrichment used in the experiment were higher than those that would be expected to occur naturally in the world's oceans, this increase in primary production should represent a maximum response of a coral reef ecosystem to natural nutrient enrichment. Kinsey (1979) has determined that metabolite rates of coral ecosystems at One Tree Island are representative of coral ecosystems in general therefore their response to nutrient enrichment might also be considered representative. If so, the most by which the productivity of a coral reef ecosystem might be expected to increase as a function of natural nutrient enrichment would be by about a factor of 1.5. Hence, while the nutrient limitation hypothesis must be considered valid because it is unquestionable that the photosynthetic process requires light and nutrients, it appears that natural nutrient enrichment can at best produce relatively small (50%) increases in production. This conclusion puts into perspective the dogma that coral reefs owe their high productivity to the highly efficient recycling of nutrients by endosymbiotic zooxanthellae (Muscatine and Porter (1977). While coral reefs do exist in nutrient poor water in terms of concentration, the *flux* of nutrients under normal conditions appears sufficient to maintain high biomass and high areal primary production. Perhaps rather than viewing coral reefs as nutrient limited systems, a more accurate interpretation may be that coral reefs are operating near their upper limit set by metabolic rates associated with the photosynthetic process rather than nutrient concentration per se. Of course within environments such as confined embayments, estuaries, etc., where nutrients may be drawn down to limiting levels, nutrients can limit productivity and benthic biomass (Smith and Jokiel 1978). This condition, however, would not apply to coral reefs which exist in unconfined environments.

If nutrients under normal conditions do not exert strong control over primary production of most coral reefs in unconfined environments, then what does? Recent work by S. V. Smith (1981) has shown that very high rates of reef calcification (11.7 kg $CaCO_3/m^2$/year) and gross primary productivity (17 g $C/m^2/d$) exist at the Houtman Abrolhos Islands (29° south latitude). These rates can be compared to average rates for reefs in general which according to Kinsey (1979) are about 5 kg $CaCO_3/m^2$/year for calcification and 7 g $C/m^2/d$ for gross primary productivity. Smith (1981) attributes the very high values at the Abrolhos Islands in spite of seasonally low temperature (20 °C) and light intensity (300 Langleys/d), to the three dimensional structure of shallow thickets of *Acropora* corals which occur there. In describing the Abrolhos transects Smith states that "virtually the entire surface of the coral transect is not only covered but stacked with photosynthetically active organisms." This result clearly shows the effect of space which may serve to double or even triple gross primary production. The same result is evident in Table 1, Part II of this paper which clearly demonstrates how differences in habitat (which in turn alters space) produce differences in primary production. Space and habitat then may be of equal or greater importance than nutrients in controlling primary production on coral reefs.

The argument that space (photosynthetically active area) is a limiting factor for coral reef primary productivity can also be interpreted as a biomass (photosynthetic) limitation argument. The more the space, the more the biomass, the more the production. The relation of space to reef productivity is also evident if one considers the bio-fouling that occurs when artificial structures (wrecks, pilings, artificial reefs, etc.) are placed on reefs. In general, such structures are quickley covered by a rich epiflora and epifauna that otherwise would not exist. Extensive bio-fouling on artificial structures on coral reefs appears to be a ubiquitous phenomenon. Clearly, in such instances nutrients in the water are not limiting and often a much greater reef biomass can be supported than that which naturally exists.

So much for the production of new organic carbon. Let us now reconsider production at higher levels in the ecosystem. We have seen from the ECOPATH model that only about 5% of the net primary production at French Frigate Shoals is passed up the food chain to higher non-benthic trophic levels. We have also seen that very high internal predation exists within the heterotrophic benthos and the reef fishes. The *P*/*R* radio of many whole reef systems is not much higher than 1.0 (Kinsey 1979) underlining the point that most of the carbon produced is respired (via predation) within the system. On occasion, however, there can also be a substantial loss of organic carbon probably in the form of offshore transport (Qasim and Sankaranarayanan 1970). Given all of these sources of loss, it is not surprising that production at the top of the food chain is so low (462 kg/km^2/year, see Part I). Thus in spite of high productivity relative to other marine and terrestrial ecosystems, coral reefs may not be very efficient in terms of producing biomass yield. The ratio of fish yield to phytoplankton primary production of those reefs for which estimates of each are available ranges between 0.0001 and 0.0008 with a mean of 0.0004 (this paper and Martin and Polovina 1982). Most of the losses described above have to do with predation (respiration is a by-product of predation). That predation is the major force regulating secondary and higher production of coral reef ecosystems is also indicated by the high level of ecotrophic efficiency estimated from the results of the ECOPATH model.

In conclusion, the answer to the question "are coral reefs nutrient limited or predation controlled" is that both processes are important, but for primary productivity, photosynthetic rate limits, space and how it is used (habitat), may be even more important than nutrients per se. For secondary and higher production, predation is clearly the major controlling factor.

Several examples from the literature illustrate the controlling effects of predation on aquatic or coral reef ecosystems. Dramatic examples include explosions in fish herbivores as a consequence of heavy exploitation of the carnivores in the Gulf of Thailand and Lake Victoria (Pauley 1979). Lower down on the foodchain, herbivores are often in close balance with plant production. Experiments using exclusion cages to protect algae from grazing often lead to rapid colonization by fleshy algae (Wanders 1977). Also the abundance of fleshy algae in most turbulent sectors of the reef is often attributed to exclusion of fish from grazing in such areas (Conner and Adey 1977). Conversely the scarcity of fleshy algae in more exposed areas of the reef is thought to be a result of grazing (Hawkins and Lewis 1982). Another effect illustrating the control of herbivory on coral reef macroalgae are the "halos" (areas of heavily grazed algae) that exist around patch reefs in so many parts of the world (Randall 1963).

The apparent balance between herbivores and algal production on coral reefs may explain why in some instances of eutrophication large increases in benthic algae have occurred. In Hawaii for example, during the late 1960's when about 4 million gallons of sewage were discharged into Kaneohe Bay daily, large mats of the benthic algae *Dictyospheria cavernosa* rapidly developed throughout portions of the bay (Banner and Bailey 1970). Herbivory, in quantity and kind, was possible unable to provide sufficient grazing pressure to control plant growth. In other polluted systems reports of algal population explosions (Benayahu and Loya 1977) may owe their existence to a similar imbalance. Given enough time these situations could possibly attain a new balance at higher rates of primary production.

In conclusion, the results of this research presented in Parts I and II and other numerous examples in the literature, suggest that in general coral reef ecosystems are regulated from the top down by forces of predation. Trophic regulation is similar to many terrestrial ecosystems particularly near the top of the food chain where carnivores control herbivore populations. On land herbivores in general are regulated by carnivores and do not keep pace with plant production explaining why the world is green (Hairston et al. 1960). On the French Frigate Shoals reef, predator control appears to generally extend all the way down the food chain. This explains why fleshy algae are so inconspicuous or rare on coral reefs. Compared to land, the reef is brown.

The conclusion that coral reef ecosystems are limited by a combination of nutrients, photosynthetic rate limits and space (habitat), and regulated by predator control is a departure from the traditional view that coral reefs are simply nutrient limited. This new hypothesis, call it the rate-space-predation hypothesis, does not refute "nutrient limitation" but rather puts it into a larger perspective in which the significance of other factors acting in combination are accounted for.

Finally, from the equilibrium or long term average perspective that we view the coral reef ecosystem, larval recruitment would not appear to be a limiting factor. While variation in larval recruitment produces variation in year class strength and is very important in the short term variation in the ecosystem, this variation averages out in the long term perspective. Further, even short term recruitment variation is probably primarily due to predation and environmental factors which affect the survival of the larvae and juveniles rather than variation in larvae production (Sale 1982; Bohnsack 1983).

Management Implications

The holistic perspective gained by attempting to analyze a coral reef ecosystem simultaneously from the top down and the bottom up, suggests several rather obvious but important principles for purposes of resource management.

1. To maximize efficiency, harvest at levels of sustained yield as low on the food chain as possible (Pauley 1979). Cropping of predators would increase potential yield. Reef invertebrates and algae present many opportunities for this strategy. In some coral reef environments this approach has been taken inadvertently (Smith and Stimson 1979). The large variation in fishery yield for coral reefs around the world (Acala and Lucharez 1982) may primarily be due to harvest at different trophic levels rather than intrinsic differences in primary production.

2. Fisheries targeted as top carnivores will serve to ease or release predation pressure on prey species. At French Frigate Shoals a tiger shark fishery could possibly help restore population levels of the endangered monk seal (*Monachus schauinslandi*) and the threatened Hawaiian green turtle (*Chelonia mydas*).

3. Reef ecosystems may be easily overfished because annual production is lower than rates suggested by levels of gross primary production and because natural mortality is high and cannot support heavy fishing mortality. It has been suggested that due to high predation, prey

stocks are already optimally exploited by predators so that even limited fishing pressure on the prey stocks can cause rapid stock decline (Pauley 1979; Ursin 1982).

4. At the level of primary and benthic secondary production, the most efficient means of stimulating production might be a combination of increased space (artificial reefs or substratum) and slight nutrient enrichment. Rapid and large scale nutrient enrichment such as that brought about by artificial upwelling, could result in choking the system by turning it green. It would be of theoretical and practical interest to gradually increase nutrients on a large scale to see if the ecosystem could slowly adapt. This might be attempted in combination with increased harvesting levels on primary producers or carnivores feeding on herbivores. The latter condition should result in higher standing crops of herbivores and corresponding higher grazing rates. Discovering the proper balance between these offsetting effects is an important problem for future research.

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A List of American and Soviet Institutions Possessing Collections of Osteological Specimens from Pinnipeds and Sea Otters

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ABSTRACT

Because different populations of the same species of pinnipeds and sea otters often have different populational parameters and histories of exploitation, modern conservation policy calls for identification of such management units below the specific level. To do so often requires analysis of large numbers of specimens from a morphological aspect, particularly by study of skeletal materials. By mutual agreement, to assist Soviet and American researchers in locating major sources of osteological specimens, we have compiled a list of the collections in the USA and USSR. Some 13,000 specimens of pinnipeds and 1,200 of sea otters, in 70 institutions, are recorded.

РЕЗЮМЕ

Разные популяции одного вида ластоногих, а также калана часто имеют разные параметры запасов и историю промысла. По этим причинам с позиций современной стратегии охраны необходимо идентифицировать такие популяции внутри вида.

В связи с этим зачастую требуется анализ большого количества морфологического материала, особенно по остеологии. По взаимному соглашению в целях окозания помощи американским и советским исследователям в определении местонахождения остеологического материала составлен настоящий список коллекций в США и СССР. Зафиксировано около 13000 экземпляров по ластоногим и 1200 по каланам в 70 учреждениях обеих стран.

INTRODUCTION

A major emphasis in modern conservation of marine mammals is on management by population or stock, because different populations of the same species quite often have different histories of exploitation and different levels of natural mortality and reproduction. A sound management policy for one population is not necessarily applicable to another population of the same species. For that reason, the International Whaling Commission and other management bodies, national as well as international, have increasingly moved to management on a stock-by-stock basis.

For many, if not most, marine mammals, populational variation and subdivision within the species are very poorly known or understood. The reasons for this are that 1) the decision for or against subdivision below the species level is based on morphology (osteology, coloration, body size and shape, etc.), and 2) morphological differences at that level are not absolute and require rigorous analysis of large numbers of specimens. Thus, modern management relies on the availability of large numbers of specimens. Unfortunately, marine mammal specimens are difficult and expensive to collect, process, and store. Consequently, most museums and other repositories possess only synoptic collections, or at best, a few dozen specimens of one or two species. For that reason, one usually must examine the specimens in many collections before reaching a conclusion on whether a particular subdivision of a species is justified. Before a collection can be used, of course, one must know what is in it; it must be cataloged and documented in a readily accessible publication or report.

Because of growing Soviet-American collaboration in research and management programs for marine mammals of mutual interest, the US-USSR Marine Mammal Project meetings in La Jolla, USA, in 1977 and in Ulan Ude, USSR, in 1978 endorsed the concept of cataloging world collections of marine mammal osteological specimens and agreed to assist and expand an existing cataloging effort by the U.S. National Museum of Natural History. This program has been underway for several years, with many major collections in the United States and Europe already documented. Collections in the Soviet Union have been included very recently and on a small scale. As the first step in a comprehensive cataloging program, specialists in the United States and the Soviet Union agreed to compile and exchange lists of collections which contain marine mammal specimens. The present list was compiled from that exchange.

METHODS

A total of 151 institutions, including universities, colleges, museums, government agencies, and oceanaria were surveyed. A list of institutions with marine mammal specimens compiled by Mead in 1973 served as a starting point for this survey. Other collections were located by reviewing catalogs of museums and educational institutions and published lists (Anderson et al. 1963;

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Katz and Katz 1965; Choate and Genoways 1975; Podolsky 1975; Wolman 1978[4]). Each institution was contacted first by telephone. If the institution had marine mammal osteological specimens (a speciman may be anything from a single bone to a complete skeleton) an estimate of the number of specimens was obtained and a checklist questionnaire was mailed to the institution in order to obtain a more detailed inventory of the collection. Eighty-five percent of the questionnaires were returned.

RESULTS

Of the institutions surveyed, 70 reported pinniped osteological specimens (Table 1), and 81 did not. Six institutions reported only total numbers of marine mammal specimens.

Of the approximately 17,300 marine mammal specimens located, about 75% were pinnipeds and 7% were sea otters; the rest were cetaceans and sirenians. As an early form of the questionnaire included only cetaceans, pinnipeds, and sirenians,[5] the numbers indicated for sea otters probably are low. The U.S. National Museum of Natural History has the largest collection of pinnipeds, totaling about 2,500 specimens; the largest collection (about 1,400 specimens) in the USSR is in the Zoological Institute of the Academy of Sciences in Leningrad.

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[5] A list of cetacean and sirenian specimens in American and Soviet collections will be presented in Volume 2 of this publication series.

Table 1.—Institutions in USA and USSR possessing pinniped and sea otter osteological specimens, as of January 1979, based on survey.

	No. of specimens		
Name of institution	Pinnipeds	Sea otters	Contact
Alaska Dep. Fish & Game Subport Bldg. Juneau, AK 99801	730	—	D. McKnight Game Research Chief
American Museum of Natural History Central Park W. at 79th St. New York, NY 10024	∼750	—	S. Anderson Curator of Mammals
Bernice P. Bishop Museum P.O. Box 6037 Honolulu, HI 96818	15	—	A. C. Ziegler Vert. Zoologist
Calif. Academy of Sciences Dep. Birds & Mammals Golden Gate Park San Francisco, CA 94118	400	16	L. C. Binford Chairman
Calif. Polytechnic State Univ. Biological Sciences Dep. San Luis Obispo, CA 93409	43	119	A. I. Roest
Calif. State University Dep. Biology Hayward, CA 94542	9	1	H. Cogswell Curator
Calif. State University Dep. Biology 6101 East 7th Street Long Beach, CA 90804	17	3	Dr. Huckaby
Calif. State University Dep. Biology 5151 State University Dr. Los Angeles, CA 90032	6	—	
Calif. State University Dep. Biological Sciences 6000 J Street Sacramento, CA 95819	18	—	J. Tilley Museum Curator
Carnegie Museum 4400 Forbes Avenue Pittsburgh, PA 15213	463	—	Curator of Mammals
Charleston Museum 121 Rutledge Avenue Charleston, SC 29401	∼4	1	A. Sanders Curator of Natural Sciences
Cornell University Bird & Mammal Museum, Bldg. 3 Ithaca, NY 14850	53	—	R. G. Bauer Curatorial Associate
Denver Museum of Natural History[1] City Park Denver, CO 80205	27	—	H. C. Wichers Curator of Mammals
Field Museum of Natural History Roosevelt Rd. at Lake Shore Dr. Chicago, IL 60605	189	—	S. Walchuk Division of Mammals
Florida State Museum University of Florida Gainesville, FL 32611	14	—	S. Humphrey
Harvard University Museum of Comparative Zoology Cambridge, MA 02138	566	—	E. Rutzmoser Curatorial Asst. of Mammals
Humboldt State University Dep. Zoology Arcata, CA 95521	81	—	R. Sullivan Vert. Zoology Museum
Los Angeles County Museum of Natural History 900 Exposition Blvd. Los Angeles, CA 90007	333	5	D. R. Patten
Louisiana State University Museum of Zoology Baton Rouge, LA 70803	1	—	J. P. O'Neal
Marineland of Florida Route 1, Box 122 St. Augustine, FL 32084	1	—	R. Jenkins

Michigan State University The Museum East Lansing, MI 48823	24	—	J. Matson
Monkshire Museum of Science Hanover, NH 03755	3	—	R. Chaffee
National Marine Fisheries Service La Jolla Laboratory P.O. Box 271 La Jolla, CA 92038	2	1	W. F. Perrin, L. J. Hansen
National Marine Fisheries Service Marine Mammal Division 7600 Sand Point Way, Bldg. 32 Seattle, WA 98115	271	3	C. Fiscus
National Museum of Natural History Division of Mammals Smithsonian Institution Washington, DC 20560	~2,500	500	J. G. Mead Curator of Marine Mammals
New England Aquarium Central Wharf Boston, MA 02110	15	1	L. Garibaldi Curator
New York State Museum Washington Avenue Albany, NY 12224	1	—	P. Connor
North Carolina State Museum P.O. Box 2281 Raleigh, NC 27611	3	—	D. Lee Curator of Mammals
North Carolina State University Dep. Zoology Raleigh, NC 27607	7	—	Dr. Barkaloo
Ohio Historical Society[1] Natural History Division Ohio Historical Center Columbus, OH 43211	3	—	C. W. Albrecht Curator of Natural History
Oklahoma State University Museum of Natural History Stillwater, OK 74074	10	2	B. Glass
Oregon Institute of Marine Biology Charleston, OR 97420	2	2	J. Hanna
Oregon State University Marine Science Center Newport, OR 97365	17	—	B. Mate
Peabody Museum of Natural History Yale University New Haven, CT 06520	66		J. Ostrom
Peabody Museum of Salem Salem, MA 01970	2	—	S. Pidugalls
Philadelphia Academy of Science 19th St and Parkway Philadelphia, PA 19103	137	—	F. B. Gill
Princeton University Museum of Natural History Princeton, NJ 08540	15	—	D. Baird Geology Dep.
San Diego Natural History Museum P.O. Box 1390 San Diego, CA 92112	130	—	R. M. Chandler Curator of Birds & Mammals
San Jose State University 125 South Seventh Street San Jose, CA 95162	103	—	J. Vollenweider Museum of Birds & Mammals
Santa Barbara Museum of Natural History 2559 Puesta del Sol Road Santa Barbara, CA 93105	85	48	C. Woodhouse Head, Marine Mammal Program
Southern Illinois University Zoology Department Carbondale, IL 62901	4	2	E. C. Gallbreath
University of Alaska Museum University of Alaska Fairbanks, AK 99701	487	8	S. MacDonald
University of California Museum of Vertebrate Zoology 2593 Life Sciences Bldg. Berkeley, CA 94720	262	28	W. Z. Lidicker, Jr. Curator of Mammals
University of California Dep. Zoology Davis, CA 95616	17	—	M. Hildebrand
University of California School of Veterinary Medicine Davis, CA 95616	10	—	L. M. Julian
University of California Biology Dep., Dickey Collections Los Angeles, CA 90024	28	—	J. Miller Curator
University of California Santa Cruz, CA 95060	~10	—	T. Dohl
University of Colorado Museum Boulder, CO 80302	14	—	S. K. Wu Curator of Zoology
University of Connecticut Dep. Biological Sciences Storrs, CT 06268	10	—	R. Dubos
University of Kansas Museum of Natural History Lawrence, KS 66044	~12	~1	R. S. Hoffman Curator of Mammals
University of Miami School of Marine Sciences 4600 Rickenbacker Causeway Miami, FL 33149	4	—	J. Reynolds
University of Michigan Museum of Paleontology Ann Arbor, MI 48104	2	—	Dr. Smith
University of Michigan Museum of Zoology Ann Arbor, MI 48104	24	—	P. Myers
University of Missouri Museum of Zoology Columbia, MO 65201	60	—	Dr. Elder
University of Montana Dep. Zoology Missoula, MT 59801	19	—	
University of New Mexico Dep. Biology Albuquerque, NM 87106	10	—	J. Finley
University of Notre Dame Dep. Biology Notre Dame, IN 46556	1	—	
University of Oregon Museum of Natural History Eugene, OR 97403	17	2	E. Gustafson
University of Puget Sound Puget Sound Museum of Natural History Tacoma, WA 98416	374	34	E. Kritzman
University of Texas, Austin Texas Memorial Museum 2400 Trinity Austin, TX 78705	~6	—	R. Martin

University of Washington Burke Museum Seattle, WA 98195	53	—	J. Rozdilsky Zoology Div.
Virginia Polytechnic Institute and State University Dep. Biology Blacksburg, VA 24061	6	—	J. Crawford
Waikiki Aquarium 2777 Kalakaua Avenue Honolulu, HI 96815	1	—	L. Taylor
Washington State University Dep. Zoology Conner Zoology Museum Pullman, WA 99164	30	-	R. E. Johnson
Moscow State University Zoological Museum Moscow, USSR	1,124	0	O. L. Rossolimo I. R. Pavlinov
Academy of Sciences of USSR Zoological Institute Leningrad, USSR	1,426	261	I. M. Gromov
Atlantic Research Institute of Fisheries and Oceanography Kaliningrad, USSR	372	0	V. A. Zheglov G. V. Rezvov I. E. Filatov
Pacific Research Institute of Fisheries and Oceanography Vladivostok, USSR	379	195	G. M. Kosygin
Magadan Section Pacific Research Institute of Fisheries and Oceanography Magadan 685013, USSR	1,247	0	G. A. Fedoseev
Petropavlovsk Section Pacific Research Institute of Fisheries and Oceanography Petropavlovsk-Kamchatka, USSR	16	0	

[1] Status of collection as of 1973.

8432

SHORT COMMUNICATION

The diet of the Brown Booby *Sula leucogaster* and Masked Booby *Sula dactylatra* on Rose Atoll, Samoa

Craig S. Harrison[1], Thomas S. Hida[2] & Michael P. Seki[2]

Ibis 126: 588–590 Received 10 February 1983

The Brown Booby *Sula leucogaster* and Masked Booby *S. dactylatra*, have pantropical ranges (Nelson 1978) and their diets have been studied on several breeding islands. Brown Boobies are considered to be inshore feeders (Diamond 1978) and have a varied diet. They feed principally on flying fish and halfbeaks in the Bahamas, but supplement this diet with prawns, parrot fish and flat-fish (Murphy 1936: 859). At Ascension Island, Brown Boobies took at least 12 prey items, including a squid *Hyaloteuthis pelagicus*, a blenny *Ophioblennius webbii*, a flying fish *Exocoetus volitans* (Dorward 1962, Stonehouse 1962) and a carangid *Trachiurops* [(*Selar*)] *crumenopthalmus* (Simmons 1967). In Australia, they fed on flying fish, squid, a mackerel *Rastrelliger kanagurta* and a carangid *Chorinemus lysan* (Serventy 1952). At Christmas Island (Indian Ocean), this species fed on a flying fish *Cypselurus bahiensis* (Gibson-Hill 1947). Our own recent study of 244 samples from the Hawaiian Archipelago (Harrison *et al.* 1983) indicated that a single squid family (Ommastrephidae) and 18 fish families (especially flying fish, carangids, and halfbeaks) were the most important components of the diet. We know of no published information concerning the diet of Brown Boobies in the South Pacific.

There are numerous published reports of the diet of Masked Boobies, which are considered to be pelagic feeders (Diamond 1978). Murphy (1936: 848) reported that they fed primarily on flying fish in South America. Flying fish *E. volitans* were also important at Ascension Island, but a blenny *O. webbii*, a trichiurid *Benthodesmus simonyi*, and an anchovy *Engraulis* spp. were also commonly taken (Dorward 1962). In Australia, this bird fed on a mackerel *Rastrelliger kanagurta* (Serventy 1952) and in the Seychelles, it fed on a flying fish *Exocoetus* spp. and squid (Vesey-Fitzgerald 1941). In the Pacific, Schreiber & Hensley (1976) reported that Masked Boobies fed primarly on flying fish and squid at Christmas Island. Our own study of 305 samples from Hawaii (Harrison *et al.* 1983) indicated that one squid family (Ommastrephidae) and 15 fish families (especially carangids, flying fish and halfbeaks) were important. We have located only anecdotal references to the diet of this species in the South Pacific: Nelson (1978) reported it ate kingfish *Regificola grandis*, a mullet *Mugil* spp., a flying fish *Cypselurus* spp. and squid at Lord Howe Island.

During the course of our work on the diets of seabirds in the Hawaiian Archipelago, we had an opportunity to examine samples from nine Brown Boobies and four Masked Boobies that were collected by regurgitation at Rose Atoll (14°32′S, 168°09′W) on 11 November 1980. These were identified to the lowest taxon possible,

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counted, measured for displacement volume and, where possible, measured for length.

The samples from Brown Boobies contained a mean of 18 prey items, ranging from eight to 46. Sample volumes averaged 73·3 ml (range 25–115 ml). Prey lengths for the 35 measured items averaged 63·5 mm (range 29–103 mm). Standard length (SL) was used for all fishes. The list of prey items (Table 1) utilizes rankings of importance to family level using a system similar to that employed by Ashmole & Ashmole (1967) in which the three commonly reported measurements of prey importance (numbers of organisms, percent occurrence, average percent volume) are equally weighted. This ranking system is described further in (Harrison *et al.* 1983). The most important prey items of Brown Boobies at Rose Atoll were juvenile forms of ommastrephid squids, goat fishes (Mullidae), and a squirrel fish *Holocentrus diadema*. The lengths of important prey items include *Symplectoteuthis oualaniensis* ($\bar{X} = 77$ mm, $n = 10$), goatfishes ($\bar{X} = 61$ mm, $n = 6$), and *Acanthurus triostegus* ($\bar{X} = 37$ mm, $n = 6$).

The four samples from Masked Boobies contained primarily flying fishes (including one *Cypselurus* spp.) and ommastrephid squids (including one *S. oualaniensis*). A single skipjack tuna *Katsuwonus pelamis* was the only other prey item identified. The samples contained an average of three prey items (range 1–6), a mean volume of 93 ml (range 35–168 ml) and a mean prey length of 74 mm (56–89 mm, $n = 4$).

Our experience with the analysis of seabird food samples from Hawaii make us wary of drawing premature conclusions based on limited sample sizes. However, our results here further underscore the relative stability of the diet of the Masked Booby

TABLE 1

Prey items identified to lowest taxon from nine Brown Booby samples from Rose Atoll, Samoa

Prey	Rank	Organisms (*n*)	% of samples in which occurred	% by volume
Fishes				
Acanthuridae	5 (tie)			
Acanthurus triostegus		18	11	4·9
Unidentified acanthurid		2	22	0·7
Carangidae	9	1	11	2·2
Coryphaenidae	8			
Coryphaena equiselis		2	11	0·8
Exocoetidae	5 (tie)	6	56	5·8
Holocentridae	4			
Holocentrus diadema		5	22	1·2
Unidentified holocentrid		5	56	1·1
Mullidae	1 (tie)	91	78	27·3
Scombridae	7			
Katsuwonus pelamis		4	22	4·9
Thunnus alalunga		1	11	1·3
Squid				
Ommastrephidae	1 (tie)			
Symplectoteuthis spp.		5	22	5·6
S. oualaniensis		7	33	18·4
Unidentified ommastrephid		16	67	18·9
Unidentified squid	10	1	11	0·2
Unidentified remains	3	6	67	6·7

throughout its range. Our results also underscore the ability of Brown Boobies to exploit apparently any prey that is available in inshore waters. Goat fishes, squirrel fishes and convict tangs *A. triostegus* are considered to be rather inshore fishes associated with the reef. In comparison with samples from Hawaii, Masked Boobies ate similar numbers of prey (3 *v.* 2·5 items per sample), but Brown Boobies at Rose Atoll ate more prey items (18 *v.* 12 items per sample) of smaller length (63·5 *v.* 94 mm, ANOVA $P < 0{\cdot}01$). The importance of goat fishes to Brown Boobies on a South Pacific island, which is paralleled in importance for many seabirds in Hawaii, indicates that future investigators of the diets of tropical seabirds should examine a reference collection to determine whether goat fishes occur in the diet. It is possible that some of the unidentified fishes from other studies (e.g., Schreiber & Hensley 1976) were goat fishes but were not recognized by laboratory personnel.

We are grateful to J. R. Shallenberger for collecting the samples and to R. S. Shomura for making this inter-agency work possible.

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8433

Encounters of Hawaiian Monk Seals With Fishing Gear at Lisianski Island, 1982

JOHN R. HENDERSON

Introduction

Interactions of marine mammals with various fisheries are documented for many species (Mate, 1980; Beverton, 1982; Contos, 1982), though studies have generally emphasized direct interactions which economically impact a fishery, take considerable numbers of marine mammals, and have high public visibility. Less apparent interactions, such as entanglement in lost or abandoned fishing gear, are more difficult to assess, yet may significantly impact some marine mammal species.

Northern fur seals, *Callorhinus ursinus*, have been observed entangled in net debris on shore and at sea (Fiscus and Kozloff[1]; Jones[2]; Scordino and Fisher[3]), and such entanglements may be a source of significant mortality for the species (Fowler, 1982). Collars of rope and plastic strapping have been reported on Cape fur seals, *Arctocephalus pusillus* (Shaughnessy, 1980), and Antarctic fur seals, *A. gazella* (Bonner and McCann, 1982). Hawaiian monk seals, *Monachus schauinslandi*, are also known to become entangled in fishing gear and other synthetic debris. Monk seals with distinctive, garrote scars have been observed, as have animals bearing net fragments and debris (Balazs, 1979; Kenyon, 1980; Gilmartin[4]). A weaned monk seal pup at French Frigate Shoals was found entangled in, and immobilized by, a piece of fishing net to the extent that drowning would likely have resulted had the animal not been freed (Andre and Ittner, 1980).

Fragments of lost or discarded fishing gear regularly wash ashore at all of the Northwestern Hawaiian Islands (NWHI). At Lisianski Island this occurs predominantly on the east (windward) side of the island and the debris includes net fragments, tangles of rope and line (some of which may be mooring line), and assorted glass and plastic floats. In 1978, Fiscus et al.[5] counted 18 pieces of netting at Lisianski which they considered could entangle a seal. Net fragments and tangles of line also foul on the reefs which extend approximately 100 m offshore on the north and east sides of the island, and remain partially submerged in the shallow (<5 m) water. The size of these fragments ranges from small (<1 m^2) pieces to virtually entire nets weighing over 100 kg. Many of these pieces have been identified as originated from Japanese trawls and gill nets (footnote 5).

From March to September 1982, a study was conducted at Lisianski Island to assess the effect of tagging on the behavior of weaned pups. Methods included individually marking all pups. During the course of this study, seals were observed to encounter fishing gear. These observations are reported here.

Observations

Presence and Accumulation of Net Debris

Those net fragments on the island which were deemed hazardous to monk seals were sampled and inventoried early in the season, and such debris which accumulated throughout the field season was similarly monitored. Assessment of the hazard to seals was subjective; criteria included size of the fragment and presence of loops or holes large enough to encircle the head of the seal. Fifty-two net fragments which had been present an unknown time were counted and 21 fragments washed ashore during the 6 months in which field personnel were on the island.

Inventory of debris included recording the size, location, color, and type of material. Samples were taken

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for subsequent determination of twine and mesh sizes.

Seals Lying on Nets

Seals of all ages often hauled out atop or adjacent to piles of net and line which were high on the beach. No records of this behavoir were maintained, though the behavior was particularly evident among molting individuals who apparently seek objects against which they can roll or rub to facilitate sloughing off old pelage.

Pups Investigating Net Fragments and Flotsam

Five weaned pups, none of which was involved in the entanglement incidents described below, were observed investigating floating net fragments. The pups swam into and around the fragments, often surfacing with mesh covering their head and neck. A sixth weaned pup was observed investigating a large net fragment which was fouled on a rock ledge. Although no entanglement occurred during any of these incidents, encounters such as these could easily result in entanglement if holes large enough to accommodate a head or flipper were present in the fragment.

Weaned pups were also frequently observed nuzzling and investigating plastic and glass floats and other flotsam, often mouthing various objects, including shards of broken glass floats. No injuries from these incidents were noticed. One pup inserted its muzzle into a 7 cm diameter plastic ring which remained tightly encircling the seal's snout for 24 hours before it was removed by field personnel.

Entanglements

Incident One

Soon after arrival at Lisianski on 17 March, field personnel observed a large mass of net approximately 25 m offshore on the east side of the island. Subsequent inspection of the net on 8 April showed that it was fouled on coral rubble in water 3-4 m deep, and the bulk of the net mass was floating. A 43 cm green sea turtle *Chelonia mydas*, and a small ulua, *Caranx* sp. entangled in the net were released.

At 1430 hours on 22 April a weaned male pup was found entangled in the same net. The pup's head and left fore-flipper were inserted through a hole in the mesh, and five to six strands encircled the neck and flipper. The pup was lying atop the net mass and not in immediate danger of drowning, but it was so firmly entangled that escape was unlikely and it probably would have starved had it not been released. The net was dragged ashore. It formed a pile 1.5 m high, 2 m in diameter, and probably weighed over 100 kg. The twine was gray polypropylene 2 mm in diameter; the stretched mesh size was 9 cm.

Incident Two

At 0830 hours on 6 May, a weaned pup was observed ashore on the north end of the island with a piece of net around its chest. The net fragment did not impede the seal's movements, but was tightly constricted about the chest, forming a 1-2 cm deep depression around the animal. The net would likely have eventually slipped off due to postweaning weight loss and the attendant reduction in girth. Nonetheless, infection and necrosis of the constricted tissue surrounding the constriction might also have occurred, or the net might have fouled on a piece of coral as the seal swam. The net fragment was removed by field personnel. The gray polypropylene fragment measured 30 × 60 cm, had a stretched mesh size of 10.5 cm, and a 2 mm twine diameter. The pup had been entangled through a hole in the web, not in a single mesh.

Incident Three

At 0830 hours on 8 May, a weaned pup was heard vocalizing repeatedly from the reef edge, approximately 100 m offshore from the east side of the island. Closer inspection revealed the male pup to be entangled in an 80 × 30 cm mass of monofilament net and 25 mm diameter polypropylene line. The net apparently had been fouled on the shallow reef for some time, and the pup had become entangled by four strands of the line, two strands each anterior and posterior to the front flippers, girdling the chest. The entire tangle was in water approximately 0.25 m deep, the tide was low, and the seal was held so tightly that had biologists not released the animal, it would almost certainly have drowned during the incipient high tide.

Incident four

At 0830 hours on 9 May, an adult female seal attended by her 26-day-old nursing pup was seen apparently entangled in a mass of net and line at the reef edge, about 75 m off the northeast side of the island. The female appeared to have several coils of line draped over her neck and back. The pup was swimming and vocalizing near the female.

Research personnel prepared equipment for restraining and releasing the female, but upon returning to the site at about 0930 hours, they found the female had freed herself and was ashore nursing her pup. The net which had entangled the female washed ashore later the same day, 200 m west of the entanglement site. The net mass comprised assorted polypropylene lines and monofilament net.

Incident five

At approximately 0900 hours on 23 June, a weaned male pup was found entangled in a net mass on the east side of the island. The net was the same one that entangled a pup on 22 April (incident one). Though the net mass had been previously dragged ashore, high tides and wave surge had moved it about 400 m north, where it was in the wash zone of the beach. The pup was lying atop the pile entangled by a twisted noose of mesh about its neck (Fig. 1). As in incident one, the pup was not in immediate danger of drowning, but was so firmly bound that escape would have been unlikely. Field personnel released the pup and retained the mesh noose. (The net was later moved high up on the beach.)

Discussion

Although the number of hazardous

nets counted on Lisianski was markedly higher in this study than counted by Fiscus et al. (footnote 5) in 1978 (52 versus 18), this amount does not necessarily represent accumulation over 4 years. Some of the nets cataloged in 1982 were found in vegetation well up the beach, and may not have been seen during the 4-day visit in 1978. Criteria by which a net was deemed hazardous may also have been less stringent in 1982 than in 1978. Nonetheless, the large number of fragments accumulating throughout the 6-month field season in 1982 indicates that floating debris is ubiquitous in the waters of the NWHI.

Twenty-six pups survived to weaning at Lisianski in 1982. When field personnel departed the island on 15 September, 25 pups were still alive. The one pup that died was once entangled (incident one), but the death was unrelated to that incident. During a 1-month field camp from 26 October to 22 November, 24 of these pups were seen.

Since all pups were bleach marked, the identity was known of all individuals observed entangled in or investigating nets. The 10 incidents reported here (4 pup entanglements, 6 observations of pups investigating debris) involved 10 different animals, 38.5 percent of the pups of the year. Three of these entanglements could have resulted in death of the monk seal had researchers not intervened. Moreover, the large percentage of pups known to have interacted with nets suggested a general propensity in pups to explore fishing debris. Entanglement of northern fur seals, *Callorhinus ursinus*, is believed to similarly result from investigative behavior by the seals rather than from accidental blundering[6]. This investigative behavior, coupled with the presence of large amounts of such debris, could lead to considerable mortality among recently weaned monk seals. The escape of an apparently entangled adult female suggests that nets and other debris may present less hazard to adults than to pups.

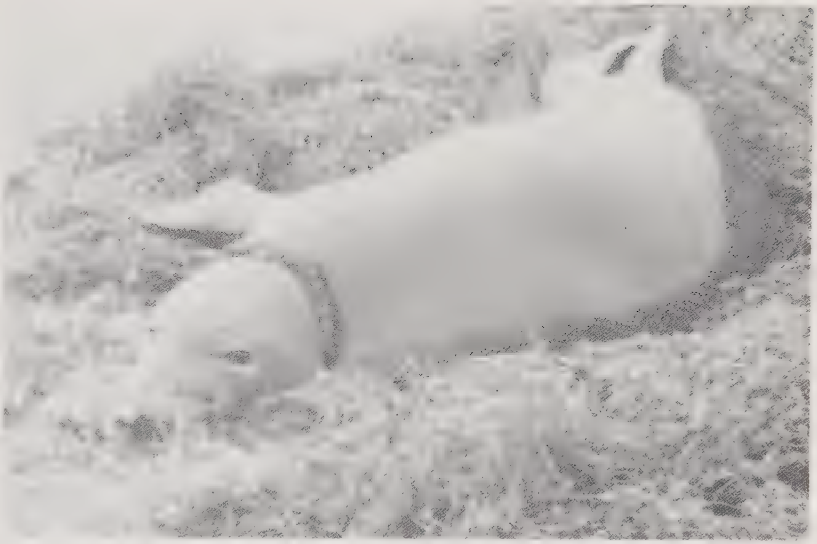

Figure 1. – Hawaiian monk seal pup (59 days postweaning) entangled in a fragment of fishing net.

Acknowledgment

Comments by Linda L. Jones and Joe Scordino improved the manuscript.

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Pleuronectiformes: Relationships

D. A. Hensley and E. H. Ahlstrom

BASICS of the current working model for evolution of pleuronectiforms were proposed by Regan (1910, 1929) and Norman (1934). In his monograph, Norman treated the flounders (Psettodidae, Bothidae, Pleuronectidae), and though he did not publish a revision of the remaining pleuronectiforms, his key and classification of the soleoids were published posthumously (1966). Norman's model and classification with the modifications of Hubbs (1945), Amaoka (1969), Futch (1977), and Hensley (1977) represent the most recent, detailed hypothesis for pleuronectiform evolution. We will refer to this as the Regan-Norman model (Fig. 358) and classification (preceding article, this volume) and consider it the working hypothesis to be reexamined using adult, larval, and egg characters.

Formation of the Regan-Norman model involved an eclectic approach, i.e., a combination of phyletic and phenetic methods. Although some of the groups currently recognized appear to be based on synapomorphies, many are clearly based on symplesiomorphies and were recognized as such by the authors. This search for horizontal relationships among pleuronectiforms using eclectic methods, with one exception, has been the only approach used in this group. The exception is the recent work of Lauder and Liem (1983) in which a cladogram for flatfishes

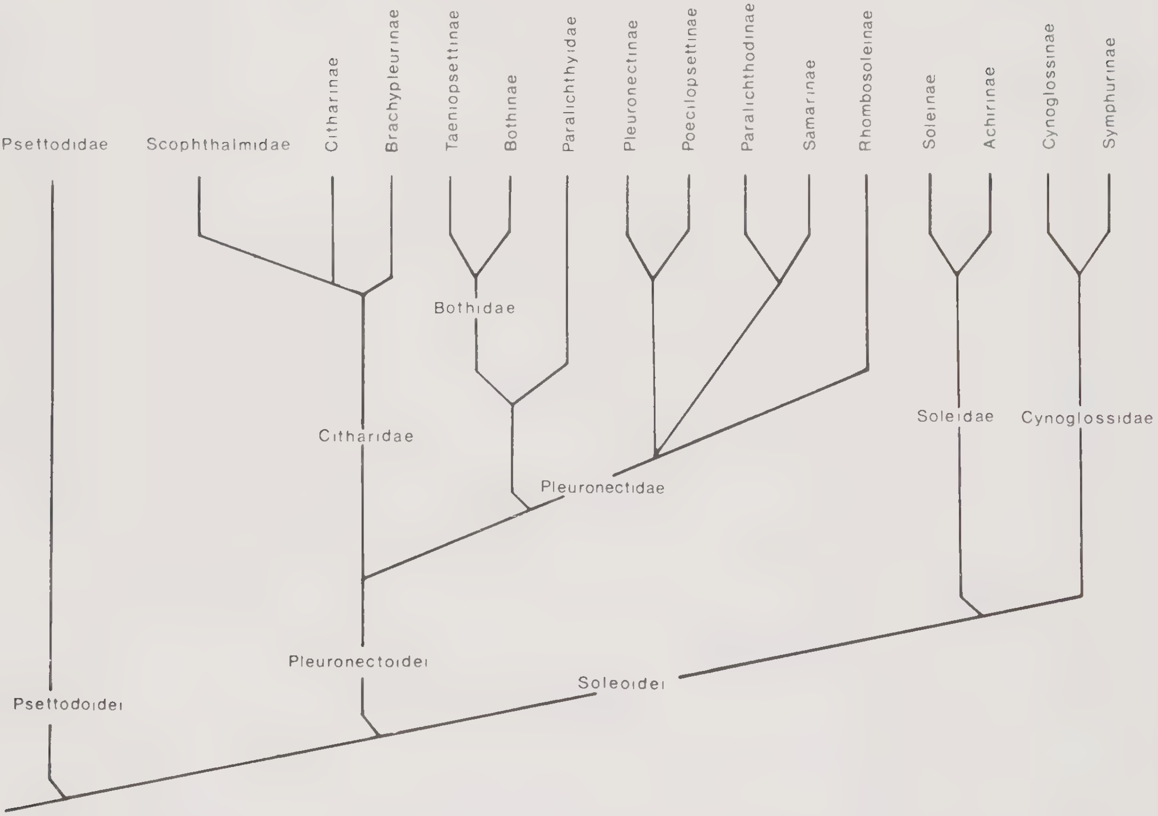
Psettodidae
Scophthalmidae
Citharinae
Brachypleurinae
Taeniopsettinae
Bothinae
Paralichthyidae
Pleuronectinae
Poecilopsettinae
Paralichthodinae
Samarinae
Rhombosoleinae
Soleinae
Achirinae
Cynoglossinae
Symphurinae
Bothidae
Citharidae
Pleuronectidae
Soleidae
Cynoglossidae
Pleuronectoidei
Soleoidei
Psettodoidei

Fig. 358. Current hypothesis for interrelationships of pleuronectiform fishes. Based on Norman (1934, 1966), Hubbs (1945), and Amaoka (1969).

is presented. However, these authors present this as a tentative hypothesis and admit that the interrelationships expressed are still problematic. Most of the character states they use are reductive, few characters were analyzed, and the authors were understandably unaware of recent character surveys, since much of this information is unpublished.

We have made the assumption that the order Pleuronectiformes is monophyletic and the sister group is the remaining percomorph fishes (sensu Rosen and Patterson, 1969 and Rosen, 1973). Although the monophyly and origin of the group is still open to question and hypotheses of multiple origins have been proposed (e.g., Kyle, 1921; Chabanaud, 1949; Amaoka, 1969), a monophyletic model with a percomorph sister group still appears to be the most parsimonious. In other words, with the information available, there appears to be no need to hypothesize multiple origins for flatfishes; to do so demands the inclusion of a great deal of convergence.

RELATIONSHIPS

The following discussion of relationships within the pleuronectiforms is cursory and preliminary. In fact, it asks more questions than it answers and illustrates that more work (particularly osteological) is needed in certain groups before the order can be subjected to an in-depth cladistic analysis. Until this work is completed, it is premature to offer a new hypothesis of interrelationships for the entire order.

Adult characters

Several criteria were used for selecting characters for discussion: (1) amount of information available on the distribution of character states; (2) characters commonly used in the past to define groups of pleuronectiforms; (3) those for which our knowledge of distributions of states is limited, but appear to indicate groupings different from those hypothesized in the working classification and which need additional study; and (4) characters which are well known in certain groups and are potentially useful for elucidating relationships within these groups. Characters and character complexes used in this study are discussed below. Characters and states are presented in Table 179.

Optic chiasma.—The relationship between the optic chiasma and ocular asymmetry of pleuronectiforms has been investigated by several workers beginning mainly with the work of Parker (1903). Hubbs (1945) examined this relationship further and presented all data from previous studies. Parker found that most fishes have a dimorphic optic chiasma, i.e., the nerve of the left or right eye is dorsal with about equal frequency (state referred to here as truly dimorphic). Exceptions to this are species of paralichthyids (sinistral) and pleuronectines (dextral) where the right or left optic nerve, respectively, is always dorsal, even in reversed individuals, i.e., the optic chiasma is monomorphic. The Soleidae and Cynoglossidae, however, retain a truly dimorphic optic chiasma. Subsequent work by Regan (1910) and Hubbs (1945) showed that in the indiscriminately dextral or sinistral *Psettodes* the optic chiasma is also truly dimorphic. In addition, Hubbs presented evidence of a third state, at least in *Citharoides* (sinistral), where the nerve of the migrating eye is dorsal even in reversed individuals. He thus interpreted the Citharidae as having a basically dimorphic optic chiasma and predicted the same for scophthalmids, although apparently no one has examined a reversed scopthalmid to test this prediction. A truly dimorphic optic chiasma as found in *Psettodes* and the soleoids has been interpreted as plesiomorphic for pleuronectiforms. The type of optic chiasma found in *Citharoides* and predicted for scophthalmids (i.e., nerve of the migrating eye always dorsal) was interpreted as an intermediate state between the truly dimorphic and the monomorphic chiasmata as found in pleuronectoids. We agree with this interpretation of polarity. However, some plesiomorphic states have been used to define groups: Psettodidae, truly dimorphic; Citharidae, basically dimorphic; Scophthalmidae, predicted to be basically dimorphic; and Soleoidei, truly dimorphic.

Major problems exist with the use of the optic chiasma for phylogenetic inference. One of these concerns the feasibility of actually determining which state exists in a group. Demonstrating the occurrence of truly dimorphic chiasmata is relatively simple. All that is needed is to show that either optic nerve is dorsal regardless of which eye has migrated; reversed individuals are not necessary. To demonstrate occurrence of the basically dimorphic state, reversals are needed and the nerve of the migrating eye must always be dorsal. Likewise, reversed individuals must be examined to show a monomorphic chiasma. Here the nerve to the right eye must be dorsal in all individuals (including reversals) of normally sinistral species and the nerve of the left eye must be dorsal in all individuals of normally dextral species. When one actually examines the data for this character (see Hubbs, 1945), states have been determined for very few pleuronectiform groups. The occurrence of the basically dimorphic state in the Citharidae was demonstrated in only one species. Of greater significance, however, is the fact that a monomorphic state has been shown for very few pleuronectoid species. Within the pleuronectoids it has been widely assumed that all paralichthyids, bothids, and pleuronectids have monomorphic optic chiasmata, and that because of this they are monophyletic and not closely related to the soleoids (truly dimorphic). It is worthy of note here that a monomorphic optic chiasma has never been demonstrated for four pleuronectid subfamilies (Poecilopsettinae, Rhombosoleinae, Samarinae, Paralichthodinae), the Bothidae, or the paralichthyid genus *Thysanopsetta.*

Ocular asymmetry.—This character (sinistral, dextral, indiscriminate) is obviously interrelated with the optic chiasma in certain groups, i.e., those with basically dimorphic and monomorphic chiasmata. The evolution of ocular asymmetry and its relationship to the optic chiasma is not well understood, although there is one major hypothesis (Norman, 1934; Hubbs, 1945) which states that primitively, pleuronectiforms were indiscriminate in ocular asymmetry and the optic chiasma was truly dimorphic. Soleoids became discriminate (soleids dextral and cynoglossids sinistral), but retained a truly dimorphic chiasma. Psettodids remained indiscriminate and truly dimorphic. Citharids and presumably scophthalmids became discriminate (scophthalmids and citharines sinistral and brachypleurines dextral) but retained some ontogenetic plasticity in regard to the optic chiasma, since reversed individuals still have the nerve of the migrating eye dorsal (basically dimorphic). The remaining pleuronectoids became discriminate (Paralichthyidae and Bothidae sinistral and Plueronectidae dextral) and evolved a monomorphic chiasma. The only exceptions with regard to ocular asymmetry are certain indiscriminate paralichthyids and pleuronectines. However, most of these indiscriminate pleuronectoids have been shown to have a monomorphic optic chiasma (a possible exception is *Tephrinectes*). It would thus appear that indiscriminate ocular asymmetry in pleuronectoids developed secondarily from discriminate ancestors (Hubbs and Hubbs, 1945).

Making phylogenetic interpretations from two states of ocular asymmetry is difficult or impossible without corroborative evidence. Thus, a statement to the effect that two or more dextral (or sinistral) pleuronectoid groups are most closely related to each other because they are dextral (or sinistral) without additional evidence of synapomorphies is circular, and may lead to the recognition of polyphyletic groups. This reasoning was the basis for the proposed close relationship in the Regan-Norman model between the Pleuronectinae and the remaining pleuronectid subfamilies (Poecilopsettinae, Rhombosoleinae, Samarinae, Paralichthodinae) and for treating the genera *Mancopsetta* and *Thysanopsetta* as members of the Bothidae and Paralichthyidae, respectively.

Ribs and intermuscular bones.—In pleuronectiforms that possess ribs, these appear to be homologous with the pleural and epipleural ribs of other teleosts, and the presence of these bones should be considered plesiomorphic for the order. Two groups lack both series of ribs, the Achirinae and apparently the Cynoglossidae. Chabanaud (1940) reports epipleural ribs in some cynoglossids but mentions no genera or species. We have not seen them in cleared-and-stained *Symphurus* species or in radiographs of several *Cynoglossus* species. Although it is still commonly believed that all soleoids lack both series of ribs (e.g., Nelson, 1976; Lauder and Liem, 1983), Chabanaud (1940, 1941) found short epipleural ribs in *Solea, Microchirus,* and *Aesopia,* and we have seen them in *Aseraggodes.*

Chabanaud (1940, 1950, 1969) found additional rib-like bones ("metaxymyostes") in certain pleuronectiforms. Some of his statements about these were in error, and it is now clear he was referring to *Bothus podas* and *Samaris cristatus* (Hensley, 1977). Amaoka (1969) found these ("intermuscular") bones in all species of his Bothidae and presented very detailed descriptions of their morphology. One of his primary justifications for elevating Norman's (1934) Bothinae to the family level was the presence of these bones in the group and their absence in Norman's Paralichthyinae. Norman considered *Engyophrys, Trichopsetta, Monolene, Taeniopsetta,* and *Perissias* to be paralichthyines. All of these genera have intermuscular bones (Amaoka, 1969; Futch, 1977; Hensley, 1977; pers. observ.) and are considered here to be bothids.

Bothid intermuscular bones are in five series. Amaoka (1969) called these series epimerals, epicentrals, hypomerals, and myorhabdoi (two series). He interpreted three of these (epimerals, epicentrals, hypomerals) as homologous with those of lower teleosts (see Phillips, 1942). The presence of these bones was the main reason both Chabanaud (1949a) and Amaoka (1969) hypothesized that pleuronectiforms were polyphyletic and that at least the Bothidae, and in the case of Chabanaud also the Samarinae, were derived from some lower teleostean group. Hensley (1977) presented arguments for interpreting the pleuronectiforms as monophyletic and the presence of intermuscular bones in at least the Bothidae as being apomorphic.

Chabanaud (1969) described intermuscular bones in *Samaris* as being in two series. However, we recently examined a cleared-and-stained specimen and found differences with Chabanaud's description. In the abdominal region, rib-like or intermuscular bones are in three series. Bones of the middle series are unbranched and in the horizontal skeletogenous septum. Most bones of the dorsal and ventral series are branched. In the region of the caudal vertebrae, there are only the dorsal and ventral series. There are none of the dorsal and ventral myorhabdoi as found in the Bothidae. Although the three series of bones found in *Samaris* resemble the epimerals, epicentrals, and hypomerals of bothids, a more detailed comparison is required before a statement about homologies can be made.

Amaoka (1969) interpreted bothids as lacking pleural and epipleural ribs, but possessing the five series of intermuscular bones. However, there is another interpretation. It is possible that Amaoka's epicentrals (limited to the horizontal skeletogenous septum of the abdominal region) and abdominal hypomerals are homologous to epipleural and pleural ribs, respectively, of other pleuronectiforms, and that the presence of myorhabdoi, epimerals, and caudal hypomerals are apomorphic states.

Postcleithra.—The absence of postcleithra was a character state, apparently apomorphic, used by Norman (1934) and subsequent authors to distinguish the Soleoidei from the Psettodoidei and Pleuronectoidei. However, an adequate survey of this character has never been made among the pleuronectoids. In a preliminary survey, we found postcleithra absent in certain pleuronectoids, i.e., the Samarinae and the bothid genera *Mancopsetta* and *Pelecanichthys.* Postcleithra are definitely present in the rhombosoleines *Oncopterus, Azygopus, Ammotretis,* and *Colistium,* but they may be absent in *Pelotretis, Peltorhamphus,* and *Rhombosolea* (Norman, 1934: fig. 25c; Chabanaud, 1949). Although lack of postcleithra in pleuronectiforms is reductive, their absence in certain pleuronectoids may indicate a closer relationship between some of these groups and soleoids than hypothesized in the Regan-Norman model. The occurrence of this specialization in *Pelecanichthys* is almost certainly an independent reduction, since this genus shows several synapomorphies with other bothids.

Vomerine teeth.—Hubbs (1945, 1946) interpreted the presence of vomerine teeth as a primitive state for the order, and we concur. However, Hubbs presented this interpretation as evidence that citharids and scophthalmids were closely related and represented an intermediate grade in pleuronectoid evolution. The presence of vomerine teeth cannot be used to infer phylogenetic relationships among pleuronectiforms.

Fin spines.—Hubbs (1945, 1946) presented the distributions for dorsal, anal, and ventral-fin spines in pleuronectiforms. *Psettodes* is the only genus with dorsal and anal spines. This genus and the Citharidae are the only flatfishes with ventral-fin spines. Hubbs properly interpreted their presence in these groups as plesiomorphic for the order. However, again, he used a horizontal or eclectic approach and inferred a close relationship between the citharid genera and interpreted the group as an intermediate grade in pleuronectoid evolution. The presence of these spines does not indicate phylogenetic (vertical) relationships.

Supramaxillae.—Supramaxillae occur in *Psettodes* and the citharids *Eucitharus* and *Citharoides* (Hubbs, 1945). In *Psettodes,* the bones are well developed and apparently present on both sides. The two citharid genera have them reduced in size, confined to the blind side, or sometimes missing. The presence of these bones is plesiomorphic for the order and should not be used to infer phylogenetic relationships.

Ventral-fin placements and base lengths.—Evolution of ventral-fin asymmetry in pleuronectiforms is not well understood. Most of our knowledge concerning the relationship between ocular and ventral-fin asymmetry has come from some rare examples of reversals in forms with asymmetrical ventral-fin morphology (see Norman, 1934). For comparative purposes, i.e., attempting to determine homologous states, it would appear to be more correct to compare ocular and blind-side ventral fins between groups rather than those of the right and left sides (see Hubbs and Hubbs, 1945). At present, there are several problems in using ventral-fin morphology to elucidate phylogenetic relationships. Most work here has dealt only with external morphology and much of this has not been sufficiently detailed or accurate. What is needed are thorough comparisons of basipterygia as well as fins. Due to the paucity of accurate and detailed studies of these structures in flatfishes, it is not possible to adequately define character states for an in-depth comparison throughout the order. Thus, ventral-fin characters were not included in Table 179. What follows is a discussion of general patterns of ventral-fin morphology.

Ventral fins with short bases and symmetrical placements have been correctly considered plesiomorphic states in pleuronectiforms, and any type of asymmetry in placement, size, shape, or meristics as having been derived from symmetrical states (e.g., Norman, 1934; Hubbs, 1945; Amaoka, 1969). Most ventral-fin characters used have involved positions of the fins relative to the midventral line and relative lengths of the fin bases. Unfortunately, symmetry (plesiomorphic states) in both of these characters has been used to define groups. Short-based fins and symmetry or near symmetry in placement and base lengths occur in *Psettodes,* the Paralichthyidae (except the *Cyclopsetta* group), the Citharidae, most soleines, most or all Pleuronectinae, and the Poecilopsettinae. States where the ocular ventral fin is on the midventral line and has a base extending farther anteriorly than that of the blind side form a continuum. Thus, groups with the base of the ocular ventral fin only slightly extended anterior to that of the blind side (origin of blind fin at transverse level of about the second or third ray of the ocular fin) are the Samarinae, possibly some Soleinae, *Paralichthodes,* the Taeniopsettinae, and *Monolene*; groups where the origin of the ocular fin is farther anterior relative to that of the blind fin are the Rhombosoleinae, all Bothinae (except *Monolene*), and possibly some Soleinae. Two groups, the Scophthalmidae and Achirinae, have both ventral-fin bases close to or virtually on the midventral line and the anterior basipterygial processes extended. The *Cyclopsetta* group has the ocular fin on the mid-

TABLE 179. CHARACTERS AND STATES FOR PLEURONECTIFORM GROUPS. Where appropriate states are indicated by underlined letters. See text and Figs. 359–364 for hypural fusion patterns.

Taxon	Optic chiasma (Truly Dimorphic, Basically Dimorphic, Monomorphic)	Ocular asymmetry (Dextral, Sinistral, Indiscriminate)	Ribs (Present, Absent)		Intermuscular Bones (Present, Absent)				Postcleithra (Present, Absent Present only in Larvae)	Vomerine teeth (Present, Absent)	Ventral-fin formula (ocular side/blind side)	Supramaxilla (Present, Absent)
			Epipleural	Pleural	Epicentrals	Hypomerals	Epimerals	Myorhabdoi				
Psettodidae	TD	I	P	P	A	A	A	A	P	P	I, 5/I, 5	P
Citharidae												
Brachypleurinae												
Brachypleura	?	D	P	P	A	A	A	A	P	P	I, 5/I, 5	A
Lepidoblepharon	?	D	P	P	A	A	A	A	P	P	I, 5/I, 5	?
Citharinae												
Citharoides	BD	S	P	P	A	A	A	A	P	A	I, 5/I, 5	P
Eucitharus	?	S	P	P	A	A	A	A	P	P	I, 5/I, 5	P
Scophthalmidae	?	S	P	P	A	A	A	A	P	P, A	6/6	A
Paralichthyidae												
**Cyclopsetta* group	?	S	P	P	A	A	A	A	P	A	5–6/6	A
***Pseudorhombus* group	?	S	P	P	A	A	A	A	P	A	6/6	A
****Paralichthys* group	M	S, I	P	P	A	A	A	A	P	A	6/6	A
Tephrinectes	M?	I	P	P	A	A	A	A	P	A	6/6	A
Thysanopsetta	?	S	P	P	A	A	A	A	P	A	6/6	A
Bothidae												
Taeniopsettinae	?	S	P?	P?	P	P	P	P	P	A	6/6	A
Bothinae	?	S	P?	P?	P	P	P	P	P, A	A	6/6	A
*****Mancopsetta*	?	S	P	P	A	A	A	A	A	A	7/5–7	A
Pleuronectidae												
Pleuronectinae	M	D, I	P	P	A	A	A	A	P	A	4–7/4–7	A
Poecilopsettinae	?	D	P	P	A	A	A	A	P	A	6/6	A
Paralichthodinae	?	D	?	?	?	?	?	?	?	A	6/6	A
Samarinae	?	D	P?	P?	P	P	P	A	A	A	5/5	A
Rhombosoleinae	?	D	P	P	A	A	A	A	P, A?	A	6–13/0–6	A
Soleidae												
Soleinae	TD	D	P	A	A	A	A	A	A	A	5/5	A
Achirinae	TD	D	A	A	A	A	A	A	PL	A	3–5/2–4	A
Cynoglossidae	TD	S	A	A	A	A	A	A	A	A	0–2/4	A

* *Citharichthys, Cyclopsetta, Etropus, Svacium*

** *Cephalopsetta, Pseudorhombus, Tarphops*

*** *Ancylopsetta, Gastropsetta, Hippoglossina, Lioglossina, Paralichthys, Verecundum, Xystreurys.*

**** *Achiropsetta* and *Neoachiropsetta* are considered synonyms.

ventral line, but the basipterygium of the blind fin is placed in a more anterior position than that of the ocular side. Another unique state is the loss of the blind ventral fin in some genera of the Rhombosoleinae, although the basipterygium of the blind side is probably still present. The Cynoglossidae are the only pleuronectiforms in which the blind ventral-fin base is oriented along the midventral line and the ocular fin is in a more dorsal position or absent. In cynoglossids missing the ocular fin, at least the dorsal process of the left basipterygium is still present.

Vertebral transverse apophyses.—Regan (1910) used the presence of transverse apophyses on caudal vertebrae as a state to distinguish his bothid subfamilies Platophrinae and Bothinae from the Paralichthyinae (=Paralichthyidae with modifications). Norman (1934) combined the Platophrinae and Bothinae into his Bothinae and Scophthalminae and again used transverse apophyses on caudal vertebrae to distinguish the bothines and scophthalmines from the paralichthyines. Amaoka (1969) used the presence of these structures to define his Bothidae and distinguish them from the other sinistral flounders he treated (Paralichthyidae, Citharidae, Psettodidae). Hensley (1977) and Futch (1977) found transverse apophyses in *Engyophrys, Trichopsetta,* and *Monolene* and suggested this as a character state indicating these genera were more closely related to the Bothidae than the Paralichthyidae. We have since found them in *Perissias.* As previously stated, Norman (1934) had placed these four genera in the Paralichthyinae. Amaoka (1969) presented the most detailed descriptions of these structures. Basically, there are two pairs of transverse apophyses on the vertebrae, an anterior and a posterior pair. They are found on many abdominal and most caudal vertebrae. Subsequently, we have found that the transverse apophyses seen by Regan (1910) and Kyle (1921: fig. 32) in the scophthalmids are very similar to those present in the Bothidae. They are similar in shape and occur in two pairs.

Amaoka (1969) interpreted the occurrence of these structures in the Bothidae as indicative of a relationship to some fish group other than the Percomorpha and used this as evidence that the Bothidae arose independently from the remaining pleuronectiforms. To support this, he cites the occurrence of similar structures in anguilliforms (Trewavas, 1932; Asano, 1962).

Recently in a preliminary survey of this character or complex in other flatfishes, we found transverse apophyses on some vertebrae in the Samarinae, Cynoglossidae, and Soleinae. However,

TABLE 179. EXTENDED.

Vertebral transverse apophyses (Present, Absent)		First neural spine (Present, Absent, Absent or Reduced)	Position of urinary papilla (Midventral, Ocular side, Blind side)	Position of vent (Midventral, Ocular side, Blind side)	Haemal arch on parhypural (Present, Absent, Rudimentary)	Articulation of parhypural with terminal half centrum (Present, Absent)	Hypural fusion pattern (1–6)	Number of autogenous epurals	Haemal spine on PU2 (Autogenous, Fused)	Total caudal-fin rays	Branched caudal-fin rays	Infraorbital lateral-line canal on ocular side (Present, Absent)
Anterior	Posterior											
A	A	P	M	M	P	P	1	1	A	24–25	15	P
A	A	P	O	O	R?	A	6	1	F	21	13	A
A	A	P	O	O	P?	P	1	2, 3?	A	23	15	P
A	A	P	O	O	R?	A	2	2, 3?	A	22–23 (usually 23)	15	P
A	A	P	O	O	A	A	4	1	F	21	14–15	P
P	P	P	O	M, B	A	A	6	1, 2?	F	16–17	13–15	P
P	P	A	B	B	A	A	6	0	F	17	11	A
A	A	P	O	B	R?	A	6	0	F	17–18 (usually 17)	10–13	P
A	A	P	O	M, B	A	A	6	0, 1, 2?	F	18	13	P
?	?	P	O	M	R?	A	1	2	F	20	14	P?
?	?	P	O	B	R?	A	1	1	F	15–16	0	A?
P	P	A	O	B	A	A	6	0	F	16–18 (usually 17)	10–13	A
P	P	A	O	B	A	A	6	0	F	15–18 (usually 17)	9–13	A
A	A	AR	O	M	R?	A	1	1	F	14–19 (usually 16–18)	13–14	A
A	A	P	O	M, B	A	A	6	1, 2?	F	17–24	10–16	P
A?	A?	AR	O	M	R	A	1	1	F	20	14–15	?
?	?	P	?	B	?	?	1	?	?	16	12	?
P	A	A	O	M	A	A	5	1?	F	16	0–12	A
A	A	AR	O	M, B	A	A	1, 4	1	F	17–20	8–15	A
P	A	A	O	M	A	A	4	1	F	16–20 (usually 18)	0–18	?
A	A	AR	O	B	A	A	1, 2?, 3	1, 2?	A	15–18 (usually 16)	11–17	P
P	A	AR	M	B	A	A	4	0, 1	F	8–14	0	A

in these groups, they occur only as one pair on the anterior end of the vertebra. In addition, the *Cyclopsetta* group has two pairs of very small lateral protuberances on most vertebrae. How to interpret the presence of vertebral transverse apophyses in pleuronectiforms is still open to question.

First neural spine.—Amaoka (1969) found that the neural spine of the first vertebra is missing in the Bothidae and interpreted this as a synapomorphy for the group, since absence of this spine is apparently rare or unknown in other teleosts. We have made a preliminary survey for this in other pleuronectiforms not treated by Amaoka. Some of this survey was based on radiographs, and due to the close proximity of the first vertebra and neurocranium, in some groups we are not sure if the first neural spine is present, absent, or greatly reduced. The states in other groups are more certain, since some cleared-and-stained material was available. A greatly reduced or missing first neural spine is not limited to the Bothidae (Table 179).

Position of the urinary papilla.—All flatfishes have a papilla on the posteroventral area of the abdomen near the anal-fin origin. Schmidt (1915, cited by Norman, 1934) commented on its position in flatfishes, claiming it was located on the ocular side in all species. However, Chabanaud (1934), Hubbs (1945), and Hubbs and Hubbs (1945) found it to be on the midventral line in *Psettodes.* In addition, Hubbs (1945) and Hubbs and Hubbs (1945) found the papilla on the blind side in the paralichthyid genera *Syacium, Citharichthys,* and *Etropus.* We have found it in the same position in *Cyclopsetta.* Another exception here may be certain cynoglossids. Menon (1977: fig. 45) shows the urinary papilla on the blind side in a species of *Cynoglossus,* but claims it is attached to the first anal-fin ray in all species of the family. A midventral position for the papilla is generalized for teleosts and plesiomorphic for pleuronectiforms.

Position of vent.—Position of the anus in flatfishes has been reviewed by Norman (1934), Hubbs (1945), and Hubbs and Hubbs (1945). A midventral position is plesiomorphic for the order. In flatfishes where the vent is on or near the midventral line, it is often very difficult to determine what state is represented. It is on the blind side in several groups, but apparently on the ocular side only in the Citharidae. Hubbs (1945) interpreted the distribution of these states as indicating that deflection of the vent to the blind side has occurred several times within the order.

Caudal-fin complex.—The caudal fin and skeleton of many species of pleuronectiforms have been illustrated and discussed (e.g., Monod, 1968; Amaoka, 1969). The caudal skeleton of *Psettodes* is reported to be the most primitive among living

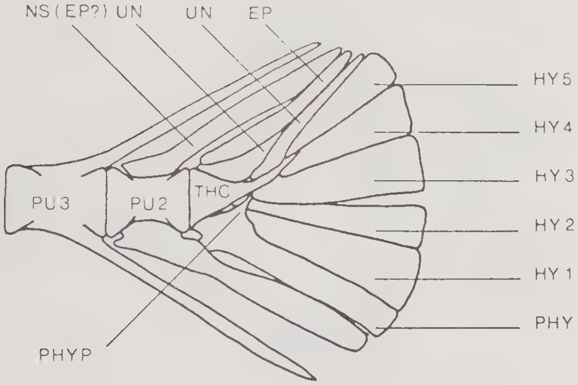

Fig. 359. Caudal skeleton of *Psettodes bennetti*. Hypural pattern 1. EP = epural, HY 1–5 = hypurals 1–5, NS = neural spine, PHY = parhypural, PHYP — parhypurapophysis, PU 2, 3 = preural centrum 2, 3, THC = terminal half centrum, UN = uroneural. Redrawn from Monod (1968).

flatfishes. It can be characterized as follows (Fig. 359): a parhypural with a haemal arch and parhypurapophysis; five autogenous hypurals; two pairs of uroneurals, i.e., pairs of stegurals and splinter bones; two epurals, the first between the neural-arch remnants of the second preural centrum; terminal half centrum, i.e., fusion of two ural centra and the first preural centrum; haemal spine of the second preural centrum autogenous; haemal spine of the third preural centrum fused; and 24–25 caudal rays, 17 principal, 15 branched. The caudal skeleton of *Psettodes* has been labelled as basically percoid (e.g., Wu, 1932; Monod, 1968; Amaoka, 1969). It should be noted here that the neural spine of the second preural centrum is interpreted as probably a captured epural, and that apparently only one free epural remains. This is one of the more important differences between *Psettodes* and all other pleuronectiforms, which have a neural spine on the second preural centrum and apparently a basal number of two epurals. There are at least two hypotheses which may explain this difference: (1) The earliest pleuronectiforms may have had three free epurals, the anteriormost becoming wedged in the neural-arch remnant on the second preural centrum (i.e., captured) and, thus forming a secondary neural spine. In *Psettodes* the remaining epurals were fused (Amaoka, 1969) or one was lost, while both were retained in the remaining flatfishes, at least primitively. (2) The earliest pleuronectiforms had two epurals, the anteriormost being captured in *Psettodes*, leaving one free epural. In the remaining flatfishes a neural spine on the second preural centrum was acquired by fusion of this vertebra with an anterior one bearing a spine. Rosen (1973) has discussed the second hypothesis to account for secondary acquisition of a neural spine on the second preural centrum and offered as evidence the frequent occurrence of double spines on the second preural centrum. Such anomalies are frequent in pleuronectiforms (see Cole and Johnstone, 1902; Barrington, 1937; Chabanaud, 1937; Amaoka, 1969; Okiyama, 1974; Futch, 1977; Fig. 360H). However, although a detailed survey for these doubled spines has never been done, it appears that doubled neural spines on this vertebra are just as frequent as doubled haemal spines.

In spite of the work that has been done on pleuronectiform caudal osteology, there is still little agreement on interpretation of some structures. We cannot solve these problems here or discuss them in great detail. Most of these differences in interpretation concern certain epaxial elements. More detailed comparative work needs to be done on these elements before homologies can be determined. For example, there is one interpretation that uroneurals occur only in *Psettodes* (Ahlstrom). However, what appear to be remnants of a stegural may remain in *Citharoides, Lepidoblepharon, Scophthalmus,* and some achirines (Fig. 361; Amaoka, 1969; Hensley, pers. observ.). Although sufficient comparative work has not been done to treat these dorsal structures across all lines of flatfishes, within certain groups we can be fairly sure of homologies, due to certain consistent patterns of placement and shape and to some larval work where fusions have been observed.

In regard to neural and haemal spines of the second preural centrum, the parhypural, and hypurals, our knowledge rests on firmer ground. Characteristics of these structures have been widely surveyed and there is much more agreement on interpretation of homologous states. We interpret autogenous neural and haemal spines on the second preural centrum, retention of a parhypurapophysis and haemal arch on the parhypural, and articulation of the parhypural with the terminal half centrum as plesiomorphic for the order.

Several patterns of fusions occur in regard to hypurals 1–4. Hypural 5 moves to an epaxial position during ontogeny in flatfishes (Figs. 360, 362), and its fate is more properly discussed in reference to fusion (or lack of it) with epurals. The most primitive condition is where hypurals 1–4 are not fused to the terminal half centrum or among themselves (pattern 1; Figs. 359, 363 upper).

There are three patterns which are slightly different from each other. The interpretation of these is not so obvious, and we are hesitant here to make statements concerning homologies between groups. One of these (pattern 2) is where hypurals 3 and 4 are fused to the terminal half centrum (Fig. 361). This pattern is shown by *Citharoides* and apparently some Achirinae. In some achirines, a somewhat different pattern (3) occurs where hypurals 2, 3, and 4 are fused to the terminal half centrum (Fig. 363 middle). A fusion of hypurals 1–4 to the terminal half centrum (pattern 4) is found in the Soleinae, Cynoglossidae, one citharid (*Eucitharus*), and two genera of Rhombosoleinae (*Peltorhamphus, Rhombosolea*; Figs. 362, 363 lower). Caudal-fin development in a soleine is illustrated in Fig. 362.

Another pattern of hypurals (5) is unique to the Samarinae (Fig. 364). There are two ways to interpret this pattern. Here the central hypurals (2 and 3 or 2–4) are fused to the terminal half centrum. However, unlike the patterns previously de-

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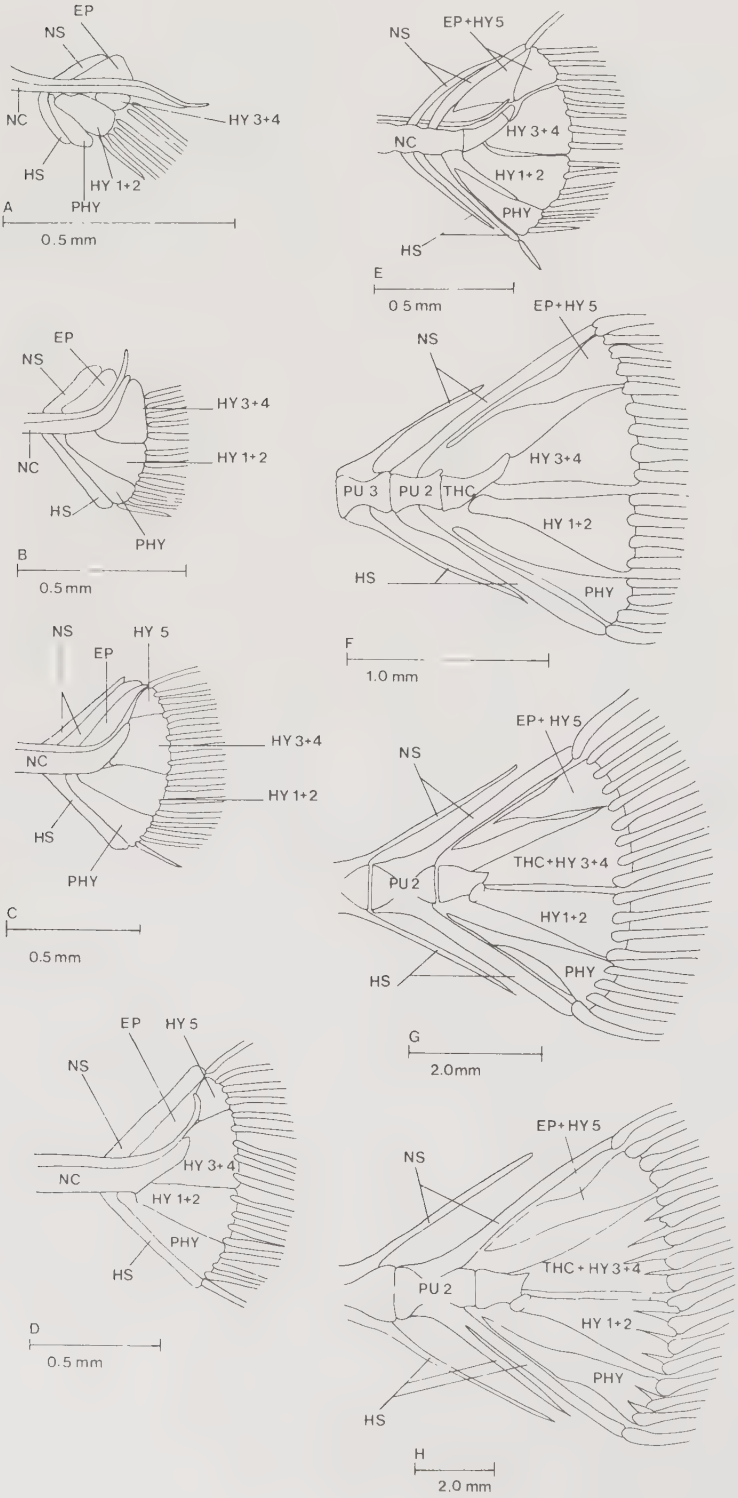
Fig. 360. Caudal-fin structure of *Engyophrys senta* larvae (A–F), juveniles and adults (G–H). Standard lengths of specimens: (A) 4.6 mm; (B) 5.5 mm; (C) 7.0 mm; (D) 7.6 mm; (E) 7.7 mm; (F) 15.3 mm; (G) 45.7 mm; (H) 82.4 mm. NC = notochord, other abbreviations as in Fig. 359. Redrawn from Hensley (1977).


EP
NS
NC
HY 3+4
HS
HY 1+2
PHY
A
0.5 mm
NS
EP+HY5
HY 3+4
NC
HY 1+2
PHY
HS
E
0.5 mm
EP
NS
HY 3+4
HY 1+2
NC
HS
PHY
B
0.5mm
EP+HY 5
NS
HY 3+4
PU 3
PU 2
THC
HY 1+2
HS
PHY
F
1.0 mm
NS
HY 5
EP
HY 3+4
NC
HY 1+2
HS
PHY
C
0.5mm
EP+HY 5
NS
THC+HY 3+4
PU 2
HY 1+2
PHY
HS
G
2.0mm
EP
HY 5
NS
HY 3+4
NC
HY 1+2
PHY
HS
D
0.5 mm
EP+HY 5
NS
THC+HY 3+4
PU 2
HY 1+2
PHY
HS
H
2.0 mm

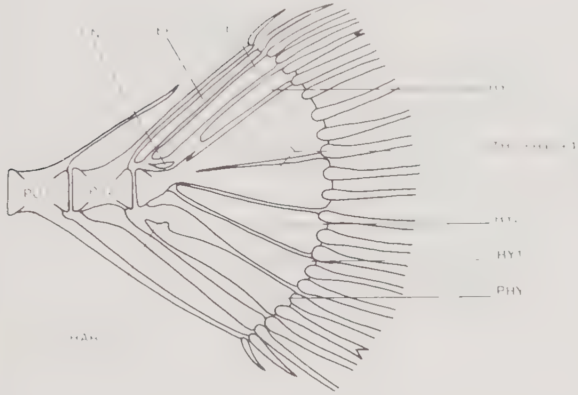


Fig. 361. Caudal skeleton of *Citharoides macrolepis.* Hypural pattern 2. HAR = haemal-arch remnant, other abbreviations as in Fig. 359. "V" on distal end of fin ray indicates dorsal- and ventralmost branched ray.

scribed, in the samarines hypural 1 does not articulate with the terminal half centrum.

The last pattern of hypurals (6) is characterized as follows (Figs. 360, 364 middle and lower): hypurals 1 and 2 are fused together forming one element which articulates with the posteroventral surface of the terminal half centrum; and hypurals 3 and 4 are fused together and to the terminal half centrum. This pattern occurs in the Pleuronectinae, Paralichthyidae (except *Tephrinectes* and *Thysanopsetta*), Scophthalmidae, one citharid (*Brachypleura*), and the Bothidae (except *Mancopsetta*). We interpret this pattern as homologous between these groups, derived, and indicative of a monophyletic origin. We will refer to these fishes as the bothoid group. Caudal-fin development in a bothid is illustrated in Fig. 360.

Although there is still some doubt concerning interpretations of certain epaxial caudal elements in flatfishes, some patterns are apparent. Most of the information indicates that at least in most pleuronectiform groups, the basal epural number is two. However, there is a small third element that appears in many species (Fig. 361; first uroneural of Amaoka, 1969). This element does not appear to be paired and its interpretation and fate in some groups is questionable. The two larger epural elements are still present in some flatfishes (Figs. 361, 363 upper), the citharids *Lepidoblepharon* and *Citharoides* and the paralichthyid *Tephrinectes.* The fate of these from the perspective of the entire order is questionable. However, it is obvious that these epurals have been reduced to one or zero in several groups. Which of these reductions are homologous is unknown. Within groups defined by other specializations, however, we are probably justified in assuming these epural reductions took the same course and are homologous states.

Although space does not allow a more detailed discussion of other caudal-fin characters, some obvious trends should be mentioned: Symmetrization—There is a marked trend among flatfishes toward dorsoventral symmetry in the caudal fin and skeleton. This has occurred by various types of fusions, losses, and secondary divisions of elements. These secondary divisions occur as scissures of varying depths in many caudal elements (Figs. 360H, 362F, 363 lower, 364 upper). Reduction of total and branched caudal rays—It has long been recognized that more primitive flatfishes tend to have larger numbers of total and branched caudal rays. Thus, *Psettodes* has a total caudal ray count of 24–25, 15 of which are branched. In many groups, caudal rays have been reduced to less than 18 and branched rays to 0–13.

Infraorbital lateral-line canal on ocular side.—In his study of sinistral flounders (i.e., Psettodidae and Pleuronectoidei) of Japan, Amaoka (1969) found ocular infraorbital bones present in the Psettodidae, two citharid genera (*Citharoides, Lepidoblepharon*), and the Paralichthyidae; they were absent from Japanese bothids. We have since done some survey work on this character in other groups not treated by Amaoka and found ocular infraorbital bones missing in additional groups (Table 179).

Examination of the Regan-Norman model using adult characters

In the following discussion, the groups and classification resulting from the current model for pleuronectiform evolution will be reexamined. The limited analysis presented here sheds much doubt on the monophyly of many of the currently recognized groups and their interrelationships. In a few cases, the evidence favoring different interpretations is so strong that these should be recognized in classifications. However, most of this analysis has produced questions and alternative suggestions that need additional study.

Psettodoidei, Psettodidae.—Nearly all of the character states used to define this group (*Psettodes,* two species) are symplesiomorphies or have been interpreted as such. Two exceptions, gill arches with groups of teeth and barbed jaw teeth, are states that Hubbs (1945) proposed as synapomorphies. Although we have no reason to doubt that *Psettodes* is a natural group, it should be redefined using character states which have been shown to be synapomorphies.

Soleoidei.—The differences between the Soleoidei and Pleuronectoidei were noted and expressed in important classifications before the works of Regan and Norman (e.g., Jordan and Evermann, 1896–1900) and they are obviously evident in the current model and classification. In most previous systematic research on pleuronectiforms, the author has concerned himself with one or the other group and assumed that the two were related only through a common ancestor near the early pleuronectiform line. The possibility, for example, that some soleoids may be most closely related to some pleuronectoids has only rarely been addressed. In any cladistic analysis of pleuronectiform interrelationships, character states used to unite the soleoids will need to be reinterpreted. Some character states

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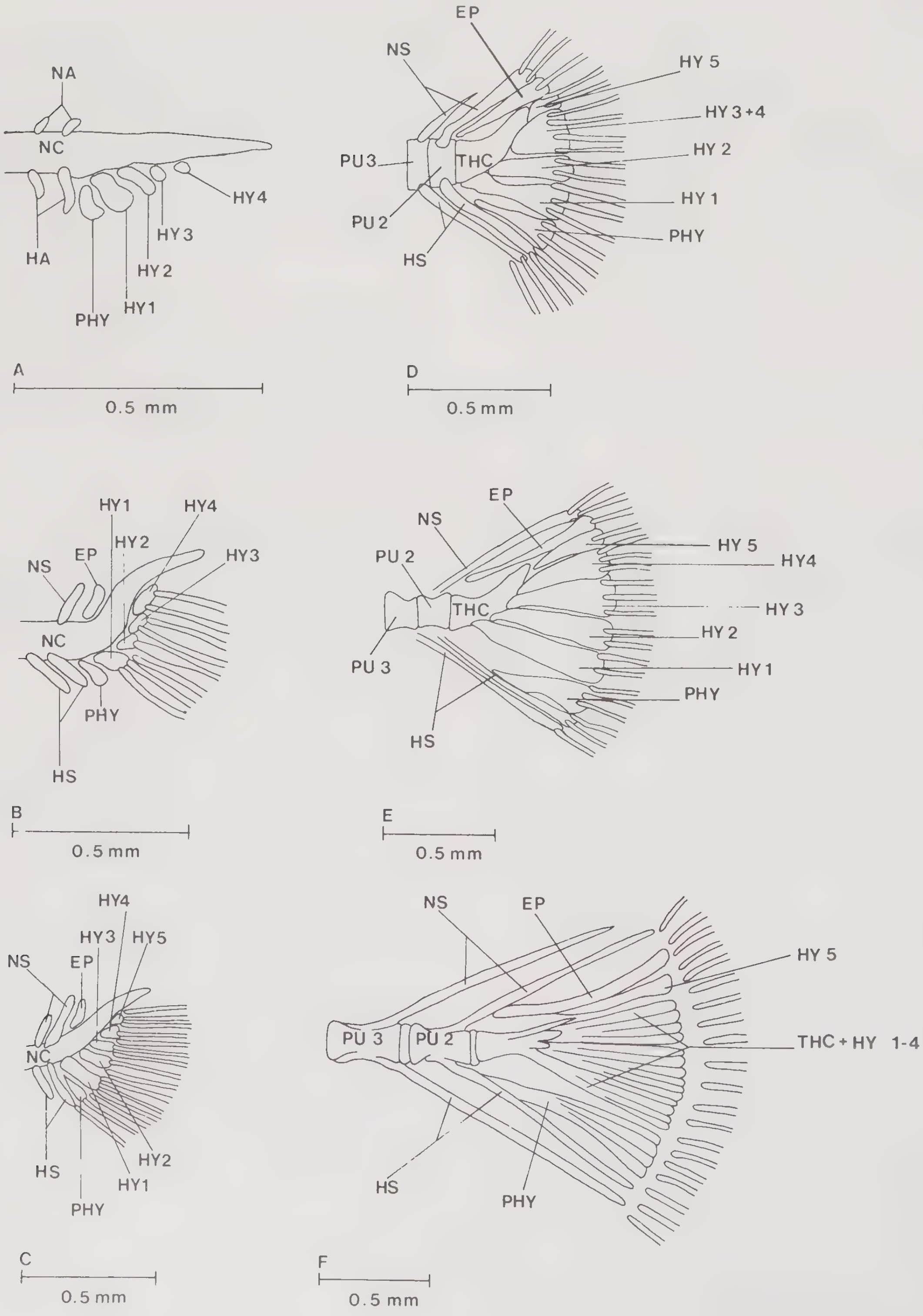
Fig. 362. Caudal-fin structure of *Solea solea* larvae (A–C), juveniles and adults (D–F). Total lengths of specimens: (A) 6.0 mm; (B) 6.8 mm; (C) 8.1 mm; (D) 11.5 mm; (E) 18 mm; (F) 470 mm. HA = haemal arch, NA = neural arch, other abbreviations as in Figs. 359, 360. Redrawn from Fabre-Domergue and Biétrix (1905).


NA
NC
HY4
HY3
HA
HY2
HY1
PHY
A
0.5 mm
EP
NS
HY 5
HY 3+4
PU3
THC
HY 2
HY 1
PU 2
PHY
HS
D
0.5 mm
HY1
HY4
HY2
HY3
NS
EP
NC
PHY
HS
B
0.5 mm
EP
NS
HY 5
HY4
PU 2
THC
HY 3
HY 2
PU 3
HY 1
PHY
HS
E
0.5 mm
HY4
HY3
HY5
NS
EP
NC
HS
HY2
HY1
PHY
C
0.5 mm
NS
EP
HY 5
PU 3
PU 2
THC + HY 1-4
HS
PHY
F
0.5 mm

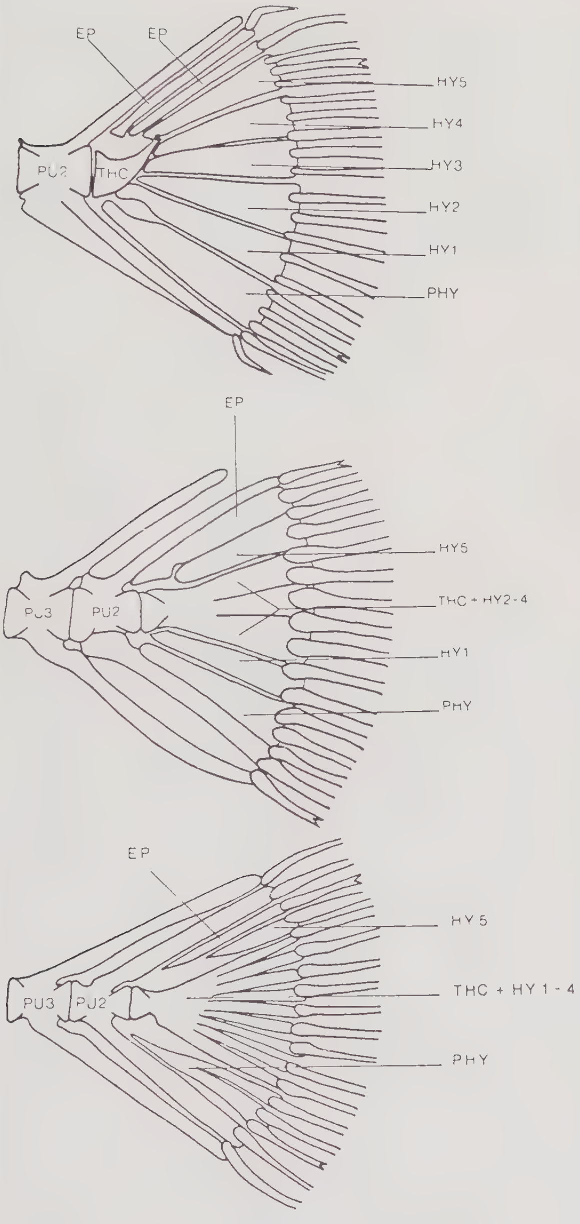


Fig. 363. Caudal skeleton of *Tephrinectes sinensis.* Hypural pattern 1 (upper); caudal skeleton of *Trinectes fimbriata.* Hypural pattern 3 (middle); and caudal skeleton of *Rhombosolea plebeia.* Hypural pattern 4 (lower). Abbreviations as in Fig. 359. "V" on distal end of fin ray indicates dorsal- and ventralmost branched ray.

used as evidence that soleids and cynoglossids are most closely related are plesiomorphic for the order (symmetrical nasal organs, dimorphic optic chiasmata), found in some pleuronectoids but dismissed as parallelisms [lower jaw not prominent, absence of postcleithra, several "soleoid characters" found in rhombosoleines, (see Norman, 1934)], or are incorrect (absence of all ribs). Other states used to unite the soleoid families include: (1) a preopercular margin covered by skin and scales; and (2) skin covering the dentary and interopercular bones being continuous across the chin, hiding the isthmus and branchiostegal rays (Norman, 1966). A covered preopercular margin is not limited to soleoids; it occurs in some rhombosoleine genera (Chabanaud, 1949; Hensley, pers. observ.). The second state as well as the absence of pleural ribs are possible synapomorphies for the group.

Cynoglossidae.—There is little doubt that the tonguesoles are monophyletic. They are unique in having the ventral fin of the blind side oriented along the midventral line and the ocular fin placed more dorsally or missing. The relationship of this family to other groups, however, is obscure (see Soleidae).

Soleidae.—The main character state proposed as uniting the two soleid subfamilies (Soleinae, Achirinae) appears to be that all species are dextral. This is still a poorly known group, and we are not prepared to make much of a contribution here. However, there are some marked differences between these subfamilies. In several characters, the Achirinae are more primitive than originally thought. Some species have hypural pattern 1, the most primitive. In species where hypural fusions have occurred, the first hypural remains free and articulates with the terminal half centrum (Fig. 363 middle). The haemal spine of the second preural centrum is autogenous (i.e., the plesiomorphic state for the order) in achirines. Uroneurals may still be present in some species. Although postcleithra are lacking in adult soleoids, at least one achirine species has them during larval development (Futch et al., 1972). Soleines differ from achirines in these characters in that they show what appear to be more derived states. The Soleinae have hypurals 1–4 fused to the terminal half centrum (Fig. 362F), the haemal spine of the second preural centrum is attached, there is no indication of uroneurals, and postcleithra have not been reported in larvae or adults. Soleines share these states with the Cynoglossidae. In addition, both groups have vertebral transverse apophyses, which are missing in achirines. The possibilities that the Soleidae are not monophyletic and the Soleinae are more closely related to the Cynoglossidae should be more thoroughly explored.

Pleuronectoidei.—Some of the character states used to define this group are plesiomorphic for the order: (1) preoperculum with free margin; (2) presence of postcleithra; and (3) presence of pleural and epipleural ribs. Some apomorphic states for the order are not limited to pleuronectoids; e.g., loss of dorsal and anal spines. The Regan-Norman model has used the position of the nasal organ of the blind side to separate pleuronectoids from soleoids and psettodids. In pleuronectoids, this nasal organ follows the migrating eye during metamorphosis. After metamorphosis, it remains near the dorsal edge of the head. This was interpreted as a specialization of pleuronectoids, except that this state does not occur in all Rhombosoleinae (i.e., nasal organs remain symmetrically placed). Thus, it is not a synapomorphy for the group, unless it can be shown that the nasal-organ symmetry in these rhombosoleines was secondarily derived from the asymmetrical state. We have not done a survey of nasal-organ symmetry, but incidental observations indicate that the supposed differences between these states (i.e., symmetrical vs asymmetrical placement) are not as great as formerly thought. Loss of a truly dimorphic optic chiasma would appear to be the only synapomorphy proposed to date uniting the pleuronectoids. However, as previously discussed, a basically dimorphic or monomorphic optic chiasma has been demonstrated in very few pleuronectoid species.

One might expect that we are well informed about the interrelationships among pleuronectoids. Unfortunately, all of the past work has used the eclectic approach. Thus, scophthalmids and citharids have been related horizontally as primitive pleuronectoids, and bothids, paralichthyids, and pleuronectids as higher groups. Again, an important character here is the optic chiasma. Two states were recognized in pleuronectoids: (1) the primitive one (for pleuronectoids) where the nerve of the migrating eye is always dorsal regardless of eye position (i.e., the basically dimorphic state); and (2) the monomorphic state characteristic of "higher" pleuronectoids where the chiasma is fixed regardless of reversals. It has been assumed that all bothids, pleuronectids, and paralichthyids show the monomorphic state. Some evidence from other characters indicates this assumption is not valid.

Due mainly to the work of Amaoka (1969) and one of us (Ahlstrom), we have a good survey of the caudal-fin complex of pleuronectoids. Patterns of hypurals 1–4 are fairly well known. The distributions of these patterns call into question much of the current evolutionary model and classification of the Pleuronectoidei. There are five patterns of hypurals in this group as defined in the Regan-Norman model: Pattern 1 (Fig. 363 upper)—This is plesiomorphic for the order. Pattern 5 (Fig. 364 upper)—This pattern is limited to the Samarinae. We interpret this pattern as a synapomorphy uniting the samarines. Pattern 2 (Fig. 361)—Within pleuronectoids this pattern seems to be limited to *Citharoides*. It is apparently derived from pattern 1. Pattern 6 (Figs. 360, 364 middle and lower)—This is an apomorphic pattern which is very distinctive. We consider it homologous in pleuronectoids where it occurs and a synapomorphy uniting these groups. Again, we are calling this group the bothoids and it includes the Pleuronectinae, Paralichthyidae (except *Tephrinectes* and *Thysanopsetta*), Scophthalmidae, Bothidae (except *Mancopsetta*), and *Brachypleura*. Pattern 4 (Fig. 363 lower)—Within the pleuronectoids this pattern is limited to certain genera of Rhombosoleinae and *Eucitharus*. Based on other characters, the homology of pattern 4 between these groups is probably not true.

Citharidae.—Many character states used to define this family (Hubbs, 1945, 1946) are plesiomorphic for the order: (1) retention of pelvic spines; (2) retention of supramaxillae (*Eucitharus* and *Citharoides*); (3) urinary papilla close to anus; (4) no union of branchiostegals; (5) retention of vomerine teeth (*Eucitharus, Brachypleura, Lepidoblepharon*); and (6) retention of short-based ventral fins. Some are plesiomorphic for the Pleuronectoidei: (1) basically dimorphic optic chiasma (at least in *Citharoides*); (2) gill membranes showing some degree of union, but still fairly widely separated; and (3) loss of dorsal and anal-fin spines. The only possible character state proposed to date that could be interpreted as a synapomorphy for this family is the position of the anus on the ocular side. Although we have not examined many specimens for this character, it appears that deflection of the anus to the ocular side is probably slight. Amaoka (1972b) examined *Brachypleura* and attempted to redefine the Citharidae. However, he still showed no synapomorphies for the group.

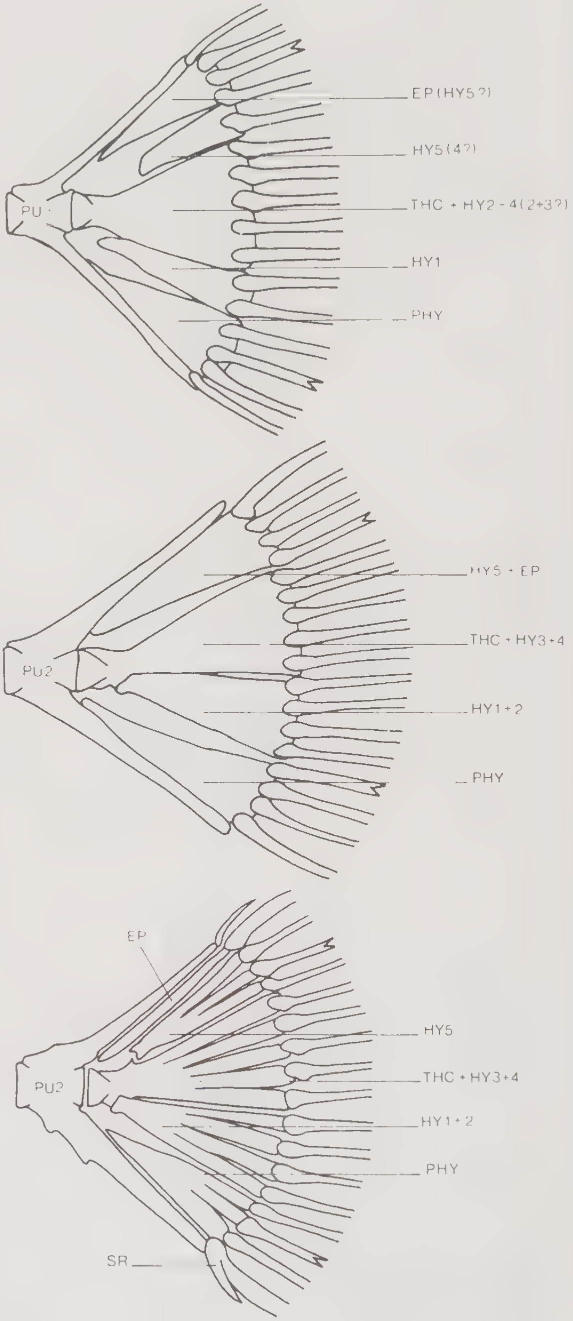


Fig. 364. Caudal skeleton of *Samariscus triocellatus.* Hypural pattern 5 (upper), caudal skeleton of *Citharichthys macrops.* Hypural pattern 6 (middle), and caudal skeleton of *Hippoglossina oblonga.* Hypural pattern 6 (lower). SR = splinter ray, other abbreviations as in Fig. 359. "V" on distal end of fin ray indicates dorsal- and ventralmost branched ray.

The family Citharidae as presently defined is a grade. Examination of the caudal osteology has shown two derived and one plesiomorphic pattern of hypurals. *Lepidoblepharon* shows pattern 1, which is plesiomorphic for the order. *Citharoides* shows pattern 2, a derived pattern (Fig. 361). This pattern could represent a state on a line leading toward pattern 6, which is shown by *Brachypleura. Eucitharus* shows pattern 4, which possibly developed independently in some rhombosoleines. The most obvious result of this is that *Brachypleura* belongs to the bothoid group, which shares the derived hypural pattern 6. In this interpretation, the character states shown by *Brachypleura* that are primitive for the order (e.g., vomerine teeth, ventral-fin spines) are also primitive for bothoids.

Scophthalmidae.—Based on ventral-fin morphology, the Scophthalmidae appear to be monophyletic. There are certain similarities in ventral-fin morphology between this family and the achirines, but these are probably superficial. Scophthalmids were previously thought to be closely related to and derived from the Citharidae (Hubbs, 1945). This hypothesis was based on certain symplesiomorphies, e.g., the low degree of fusion of the gill membranes and the presence of vomerine teeth. The Scophthalmidae show hypural pattern 6 and are thus members of the bothoid group.

Paralichthyidae.—Norman (1934) basically defined the Paralichthyinae (=Paralichthyidae with modifications) on external pelvic-fin morphology and vertebral structure (absence of transverse apophyses). The group was supposed to have the ventral fins nearly symmetrical in position and base lengths, or the ocular fin on the midventral line and its base slightly extended anteriorly. Symmetries in ventral-fin position and base lengths are plesiomorphic for the order and bothoids. Norman's paralichthyid genera with an ocular ventral fin on the midventral line and its base extended anteriorly are bothids (i.e., *Trichopsetta, Engyophrys, Taeniopsetta, Monolene, Perissias*).

Amaoka (1969) presented a more thorough, detailed definition of the family. However, many or most of the character states he used appear to be plesiomorphic for bothoid fishes (i.e., those defined by hypural pattern 6). A second limitation of Amaoka's work on this group is that it was limited to three genera (*Paralichthys, Pseudorhombus, Tarphops*). An important change in Norman's classification was made by Amaoka when he removed *Taeniopsetta* from the Paralichthyidae and placed it in the Bothidae. Hensley (1977) and Futch (1977) did the same for *Monolene, Engyophrys,* and *Trichopsetta.*

We have now examined some characters in the remaining Paralichthyidae, and additional changes are required in the composition of this group. In a survey of caudal-fin structure, it was found that *Thysanopsetta* and *Tephrinectes* show the most primitive type of hypural pattern (1; Fig. 363 upper). These two genera are much more primitive than expressed in the current classification and definitely do not belong to the bothoid group.

Within the remaining Paralichthyidae another group is discernable. This is composed of *Cyclopsetta, Syacium, Citharichthys,* and *Etropus,* i.e., the *Cyclopsetta* group. States for two complexes of characters, ventral-fin morphology and urinary-papilla position, are unique to this group and interpreted as synapomorphic. Arrangement of caudal-fin rays in the *Cyclopsetta* group is also unique and probably apomorphic (Fig. 364 middle). All species have 17 caudal rays, none of which are supported by preural, neural or haemal spines. It should also be noted that the fifth hypural has fused with an epural. This fusion has been observed in larval development (Tucker, 1982; Ahlstrom, pers. observ.). However, fusion of the fifth hypural and one or more epurals has apparently occurred several times in pleuronectiforms, possibly including the bothoids (e.g., see Fig. 360). A detailed analysis of relationships between the *Cyclopsetta* group and other bothoids is not possible here. However, some character states may indicate a close relationship with bothids (absence of first neural spine, presence of vertebral transverse apophyses).

Amaoka (1969) and one of us (Ahlstrom) recognized another group within the Paralichthyidae composed of *Pseudorhombus, Tarphops,* and *Cephalopsetta,* i.e., the *Pseudorhombus* group. We interpret these genera as more specialized in certain characters than most other members of the family. Species of this group usually have a total caudal ray count of 17, the epural is fused to the fifth hypural, and they lack a splinter ray on the ventralmost caudal-fin ray. With the exceptions noted above (the primitive non-bothoid genera *Tephrinectes* and *Thysanopsetta* and the *Cyclopsetta* group), the remaining paralichthyids of the Regan-Norman classification (what we are calling the *Paralichthys* group) have the apparently plesiomorphic states of 18 caudal rays, at least one free epural (except in one species of *Hippoglossina* (Sumida et al., 1979)), and a splinter ray on the ventralmost caudal-fin ray (Fig. 364 lower). The splinter ray is probably a remnant of a ray lost through fusion with an adjacent ray (Okiyama, 1974). The *Pseudorhombus* group may be definable by synapomorphies but a detailed analysis has not been done.

After removal of the bothids (*Trichopsetta, Engyophrys, Taeniopsetta, Monolene, Perissias*) and the primitive non-bothoid genera (*Tephrinectes, Thysanopsetta*), recognition of the *Cyclopsetta* group as monophyletic, and recognition of the *Pseudorhombus* group as possibly monophyletic, few of the original paralichthyid genera remain. We have been referring to these as the *Paralichthys* group (*Ancylopsetta, Gastropsetta, Hippoglossina, Lioglossina, Paralichthys, Verecundum,* and *Xystreurys*). At least most of the character states known for these remaining genera are plesiomorphic for the order (e.g., symmetrical ventral-fin states) or for bothoids (e.g., usual presence of at least one free epural). The *Paralichthys* group is probably not monophyletic.

Bothidae.—Norman (1934) defined the Bothinae (=Bothidae with modifications) on the basis of a high degree of ventral-fin asymmetry and the presence of vertebral transverse apophyses. The ocular ventral fin was said to be on the midventral line with its base extending anteriorly to the urohyal. Norman excluded *Taeniopsetta, Engyophrys, Trichopsetta, Monolene,* and *Perissias* from this group because the base of the ocular ventral fin, although on the midventral line and somewhat longer than that of the blind side, does not extend to the urohyal.

Amaoka (1969) examined many bothid genera and redefined the family using more characters. Most of the characters stressed by Amaoka have now been examined in other bothoids. These are discussed below:

Ventral-fin asymmetry.—In bothids the ocular fin base is on the midventral line, elongated, and has its origin anteriorly placed relative to the base of the blind fin. Within the bothoids this combination of states appears to be derived and unique.

Preorbital on blind side.—This bone is absent in the Bothidae. It appears to be present in all other bothoids (Pleuronectinae not examined for this character). Based on this comparison, we interpret the loss of this bone a derived state within the bothoids defining the family Bothidae.

Infraorbital bones of the ocular side.—All bothids have an ocular preorbital bone but lack the remainder of the series. The presence or absence of the ocular preorbital has not been surveyed in most bothoid groups. However, an ocular infraorbital lateral line is present in most bothoids. In addition to the Bothidae, it is missing in *Brachypleura* and the *Cyclopsetta* group.

Intermuscular bones.—We interpret the presence of at least two of the series of these bones (myorhabdoi) as a derived state unique to and defining the Bothidae.

First neural spine.—Although the first neural arch is present, the neural spine is missing in the Bothidae. It is present in all other bothoids except the *Cyclopsetta* group.

Vertebral transverse apophyses.—All bothids have two pairs of transverse apophyses on most vertebrae. As previously discussed, how to interpret these on the pleuronectiform level and within the bothoid group is questionable. Within the bothoids well-developed and very similar structures occur only in the Bothidae and Scophthalmidae. Very small transverse apophyses also occur in the *Cyclopsetta* group.

Based on these characters, the Bothidae appear to be monophyletic and definable by synapomorphies in at least three characters or complexes: (1) loss of the preorbital on the blind side; (2) presence of myorhabdoi; and (3) asymmetrical states of ventral-fin morphology.

Since Amaoka's (1969) work, we have examined the remaining genera not examined by him that have been considered bothids (i.e., *Grammatobothus, Lophonectes, Pelecanichthys, Mancopsetta*). All of these except *Mancopsetta* are bothids. *Mancopsetta* exhibits the following character states: (1) hypural pattern 1, i.e., the most primitive type; (2) presence of pleural and epipleural ribs, but no myorhabdoi or other intermuscular bones in the caudal region; (3) at least one free epural (none in adult bothids); (4) anus on midventral line (clearly on blind side in bothids); (5) no vertebral transverse apophyses; and (6) seven rays in the ocular ventral fin, 5–7 in that of the blind side (six in both fins in bothids). These are all characters in which *Mancopsetta* differs from the Bothidae. Due to the primitive hypural pattern, it is not a bothoid (see Rhombosoleinae).

Amaoka (1969) analyzed intergeneric relationships of Japanese bothids. However, his analysis was eclectic and did not include all genera (i.e., *Engyophrys, Trichopsetta, Monolene, Perissias, Grammatobothus, Lophonectes*, and *Pelecanichthys* were not examined). He recognized two subfamilies, the Taeniopsettinae and Bothinae. He erected the first subfamily for *Taeniopsetta*. Hensley (1977), Futch (1977), Evseenko (1977, 1981), and Amaoka (1979) implied that *Engyophrys* and *Trichopsetta* should be included in the Taeniopsettinae. This was done on the basis of larval characters and ventral-fin morphology. Most of the states used to define the Taeniopsettinae were considered by Amaoka (1969) to be plesiomorphic at the family level. Three characters were emphasized: (1) degree of anterior extension of the base of the ocular ventral fin; (2) shape of the ventral (sciatic) area of the urohyal; and (3) number of suborbital bones on the blind side. In the taeniopsettines, the origin of the blind ventral fin is at the same transverse level as the second ray of the ocular ventral fin, i.e., the base of the ocular fin is only slightly elongated. In the Bothinae, extension of the base of the ocular fin is greater and the origin of the blind fin is on the same transverse level as the third or fourth ray of the ocular fin. Obviously, the taeniopsettine state here is the more plesiomorphic. *Engyophrys, Trichopsetta, Monolene*, and *Perissias* show this state. *Taeniopsetta* has a broad, truncate margin on the sciatic part of the urohyal. In bothines, this area of the urohyal is pointed. Amaoka (1969) clearly showed that the plesiomorphic state for bothoids is closer to the condition shown in taeniopsettines. *Engyophrys, Trichopsetta*, and *Perissias* show the taeniopsettine condition, *Monolene* the bothine state. Amaoka (1969) noted an apparent trend among bothoids in reduction of the number of suborbital bones of the blind side. This reduction may have occurred in several bothoid groups and interpretation of this character is not clear. Thus, infraorbital counts for bothoids are as follows (preorbital + suborbitals): Scophthalmidae 1 + 5; *Brachypleura* 1 + 0; *Paralichthys* group 1 + 4–5; *Pseudorhombus* group 1 + 5–7; *Cyclopsetta* group 1 + 5–6; and Bothidae 0 + 3–5. Pleuronectines were not examined for this character. The most common count in bothoids other than bothids is 1 + 5–7. Thus, there is some evidence that the basal or plesiomorphic count for bothids may be five suborbitals on the blind side. Among bothids this count apparently occurs only in *Taeniopsetta* and *Pelecanichthys. Engyophrys, Trichopsetta, Perissias*, and *Monolene* have three suborbitals on the blind side. In summary, there is good evidence, at least for the first two characters discussed above, that the Taeniopsettinae show states that are plesiomorphic for the family and may not be monophyletic.

Pleuronectidae.—Norman (1934) considered this family to be one of the "higher" flatfish groups, i.e., those with a monomorphic optic chiasma. Hubbs (1945) basically followed this interpretation, but showed that two of Norman's pleuronectid genera, *Brachypleura* and *Lepidoblepharon*, possessed some primitive states not shown in other pleuronectids. These two genera were removed by Hubbs and placed in his family Citharidae.

Norman (1934) defined the Pleuronectidae as being dextral and having eggs without oil globules. Basic to his concept of this family were the assumptions that all members were monomorphic in regard to the optic chiasma and that nearly all species were discriminately dextral. He divided the family into five subfamilies. All members of the Poecilopsettinae, Paralichthodinae, Samarinae, and Rhombosoleinae, as presently interpreted, are discriminately dextral, i.e., sinistral individuals occur so rarely in any one species that they can be considered anomalies. Most species of Pleuronectinae are also discriminately dextral. The few exceptions have probably returned to indiscriminate ocular asymmetry secondarily (Hubbs and Hubbs, 1945). We have no reason to doubt Norman's or Hubbs' assumption that the Pleuronectinae have a monomorphic optic chiasma. However, as previously discussed, there are no data showing this for the other pleuronectid subfamilies. Uniting these groups in the family Pleuronectidae appears to have rested only on ocular asymmetry. We have surveyed these subfamilies for various characters and are confident that the Pleuronectidae as currently defined are not monophyletic. In fact, four of the pleuronectid subfamilies are not bothoids as we define the group. However, what the true relationships of these groups are is unknown. We discuss these subfamilies individually:

Poecilopsettinae.—We have examined radiographs of specimens of *Poecilopsetta* and *Nematops.* These genera have hypural pattern 1, at least one free epural, 20 caudal rays, and what appears to be a haemal-arch remnant on the parhypural. The caudal structure here is primitive compared to the bothoids and these fishes do not belong to that group. Poecilopsettines are poorly known and character states defining the group or relating it to others have not been investigated.

Paralichthodinae.—*Paralichthodes algoensis* has hypural pattern 1 (Ahlstrom, pers. observ.) and does not belong to the bothoid group. Its relationships to other groups are unknown.

Samarinae.—Since Hubbs' (1945) removal of *Brachypleura* and *Lepidoblepharon* from this group, it has been composed of *Samaris* and *Samariscus.* We have not done a detailed study of these genera, but some characters we have examined are worthy of note: (1) These genera show a unique hypural pattern (5; Fig. 364 upper). We interpret this pattern as derived relative to pattern 1 and as indicative that the group is monophyletic. Using this pattern to relate the group is more difficult; however, one of us (Ahlstrom) noted that in late-stage larvae of *Samariscus,* hypural pattern 1 is present, and fusions resulting in pattern 5 must occur very late in development. This is evidence that pattern 5 may have evolved directly from pattern 1 and does not represent a modification of the bothoid pattern 6. (2) Samarines are the only pleuronectiforms known other than the Bothidae to have intermuscular bones, although they do not have the two series of myorhabdoi as found in bothids. We have not done a detailed study of these bones in samarines, but they appear very similar to the epimerals, epicentrals, and hypomerals of bothids. (3) Samarines, cynoglossids, and soleines have an anterior pair of well-developed transverse apophyses on many vertebrae. Two pairs of these structures are found in the Bothidae and Scophthalmidae. (4) The Samarinae, Soleoidei, and *Mancopsetta* lack postcleithra, at least in adults. How to interpret these last three character states is open to question. Are three of the series of intermuscular bones homologous in samarines and bothids? Are the anterior vertebral transverse apophyses homologous between all of the groups? Do some of these character states indicate a close relationship between samarines and some soleoids (i.e., cynoglossids and soleines)? Our tentative hypothesis is that the samarines are a line that is at least independent from the bothoids. Here we are obviously stressing caudal characters. The corollary of this is that we are interpreting similarities between samarines and bothoids in intermuscular bones and vertebral transverse apophyses as homoplasies.

Rhombosoleinae.—The main character states used by Norman (1926, 1934) to define this subfamily were the high degree of asymmetry in the ventral fins and the absence of pectoral radials. The ocular ventral fin is on the midventral line and its base is considerably extended. The blind ventral fin is short based or missing. Another interesting characteristic of this group is that several genera show high numbers of fin rays in the ocular ventral fin. There is a great deal of morphological diversity in rhombosoleines. Some genera appear fairly generalized in many characters (*Oncopterus, Psammodiscus, Rhombosolea, Azygopus,* and *Pelotretis*); others are more specialized (*Colistium, Peltorhamphus,* and *Ammotretis*). Many of the specializations in the latter genera are similar to those in some soleoids. This has been interpreted as parallel evolution (Norman, 1934; Hubbs, 1945). Norman apparently had some doubts about aligning this group with the Pleuronectinae. He realized that Parker's (1903) examination of one specimen of *Oncopterus darwinii* in his survey of optic chiasmata did not prove the group to be monomorphic in this character. This group has still not been studied in detail. It may be monophyletic, but its relationship to other flatfishes is unknown.

We have examined the caudal skeleton of all rhombosoleine genera except *Psammodiscus.* They show hypural patterns 1 and 4 (Fig. 363 upper and lower). Assuming the group is monophyletic, there are two implications here: (1) The primitive pleuronectiform hypural pattern 1 is also plesiomorphic for the Rhombosoleinae, and the derived pattern 4 arose within the group independently from the same pattern in the Soleinae, Cynoglossidae, and *Eucitharus.* (2) The Rhombosoleinae are not bothoids and should not be aligned with the Pleuronectinae.

The possibility has recently become apparent that *Mancopsetta* may be most closely related to the Rhombosoleinae. All known specimens of *Mancopsetta* are sinistral and it has been considered a bothid. However, it shares certain character states with at least some rhombosoleines. This genus has ventral-fin ray counts of 7 on the ocular side and 5–7 on the blind side. Although not strictly limited to the rhombosoleines, these high counts, at least in the fin of the ocular side, are characteristic of at least four rhombosoleine genera. The eyes are densely scaled in *Mancopsetta* and in *Azygopus* and *Pelotretis.* However, scaled eyes are found in some genera of other groups also (e.g., some pleuronectines). Andriashev (1960) and Penrith (1965) have both remarked on a fleshy lip-like structure which overhangs the anterior end of the upper jaw in *Mancopsetta.* One of the soleoid-type characteristics exhibited by the more specialized rhombosoleines is the dorsal fin originating in a rostral hook that overhangs the mouth. In the more generalized genera, there is no rostral hook and the dorsal fin originates at some posterior position. In at least one of these generalized genera (*Azygopus,* the only one examined for this character) there is a fleshy structure (possibly a precursor to the rostral hook?) overhanging the anterior end of the upper jaw which is very similar to that in *Mancopsetta.* Obviously more comparative work needs to be done here. However, it is possible that *Mancopsetta* and the Rhombosoleinae may form a monophyletic group with an indiscriminately dextral or sinistral common ancestor.

Pleuronectinae.—Norman (1934) stressed two character states in defining this subfamily: (1) lateral line well developed on both sides of the body; and (2) olfactory laminae parallel (except in *Atheresthes*), without rachis. A well-developed lateral line on both sides of the body is plesiomorphic for the order and bothoids. We have not examined olfactory laminae or attempted to analyze distributions of states for the character.

We have shown that the Pleuronectidae is probably not monophyletic, due to the inclusion of the four non-bothoid subfamilies. The subfamily Pleuronectinae is the only bothoid group in Norman's Pleuronectidae. Members of this subfamily are dextral or apparently secondarily indiscriminate (Hubbs and Hubbs, 1945). They apparently have a monomorphic optic chiasma. However, most character states which species of this subfamily share appear to be plesiomorphic for the order or bothoids, e.g., symmetrical or nearly symmetrical ventral-fin placement and fin-base lengths, anus on or close to the midventral line. We have examined the caudal osteology of about half of the pleuronectine genera. All have the bothoid hypural pattern (6) and one or possibly two free epurals. We have found no synapomorphies in the caudal fin for this group.

Larval characters

In the previous discussion, many doubts were raised concerning pleuronectiform interrelationships as expressed in the Regan-Norman model. Unfortunately, larvae for many of these groups are unknown. A second problem is that surveys for many characters where larvae are known have been incomplete and inconsistent. Most descriptive larval research has dealt with characters useful for identification and has not involved comparative work of sufficient detail to determine homologous states. Such work is sorely needed before distributions of homologous states can be determined for many characters.

Below is a list and discussion of certain characters and complexes. Selection of these was based mainly on the amount of available information.

Preopercular spines.—The presence of preopercular spines appears to be plesiomorphic for the order and some pleuronectiform groups. This is based on the observation that the state is widespread among flatfish and percomorph larvae.

Neurocranial spines.—Spines occur in some regions of the neurocranium in some pleuronectiform larvae. Most of these are said to occur in the otic or frontal regions. However, determining homologies here is difficult due to a general lack of detailed osteological study of the bones carrying these spines. Spines in the otic and frontal regions appear to be of two types. One of these is where spines are associated with neurocranial ridge systems. These are known for larvae of achirines (Houde et al., 1970; Futch et al., 1972), some scophthalmids (Jones, 1972), and some pleuronectines (Pertseva-Ostroumova, 1961). In the second type, spines occur singly or in small groups but are not part of a pronounced ridge. These have been said to occur on various bones of the otic region (epiotics, autosphenotics, autopterotics) or on the frontals. Tucker (1982) was not able to determine the origin of such spines in the larvae of *Citharichthys* and *Etropus* and referred to them as frontal-sphenotic spines. Although thorough studies are needed before neurocranial spines can be used to infer or test pleuronectiform interrelationships, certain patterns are noteworthy: (1) Spines that are not part of some pronounced ridge system appear to be limited to some bothoids (some species of the *Paralichthys* group, *Cyclopsetta* group, *Pseudorhombus* group, Scophthalmidae, Pleuronectinae, and Bothidae). (2) Within the Bothidae, only the larvae of *Engyophrys, Taeniopsetta,* and *Trichopsetta* (Taeniopsettinae; larvae of *Perissias* are unknown) are known to have otic spines (Amaoka, 1979). In these genera, the spines are on the same bones (epiotics and autosphenotics) and are probably homologous. (3) Within the *Cyclopsetta* group, a relatively well-developed otic or frontal spine occurs in *Cyclopsetta* and *Syacium* (Aboussouan, 1968b; Gutherz, 1970; Ahlstrom, 1971; Futch and Hoff, 1971; Evseenko, 1979), while series of small spines occur in *Citharichthys* and *Etropus* (Tucker, 1982).

Urohyal, basipterygial, and cleithral spines.—Spines on these bones are limited to certain genera of the Bothidae. Thus, they are considered apomorphic at the pleuronectiform and bothoid levels of universality.

Early-forming elongated dorsal-fin rays.—The presence of elongated dorsal-fin rays in pleuronectiform larvae has been extensively and justifiably used for identification purposes. However, use of these structures for phylogenetic interpretations is presently difficult and generally premature. There are several reasons for this. Surveys for these characters are inadequate, since larvae for many groups are unknown. Characters and character states have never been adequately defined to allow proper comparisons to be made. The only pattern here that is clear and phylogenetically interpretable is the state in bothids. All species of this family for which larvae are known show elongation of only the second dorsal-fin ray. This state is known only in this family and thus appears to be apomorphic within the order and bothoids.

Early-forming elongated ventral-fin rays.—Ocular ventral-fin rays which are elongated relative to those of the blind side are limited to certain species of the *Cyclopsetta* group. Due to the restricted occurrence of these, they are probably apomorphic for the order and bothoids. However, within the *Cyclopsetta* group, the distribution of elongated ocular ventral-fin rays does not conform to generic groups based on adult morphology. At least one species of cynoglossid is known to have elongated rays in the ventral fin of the blind side (Kyle, 1913; Padoa, 1956k).

Size at metamorphosis.—Most flatfishes metamorphose in the size range of ca. 10–25 mm. When size at metamorphosis has been discussed in regard to evolution in pleuronectiforms, the usual hypothesis has been that certain species and groups have evolved mechanisms for prolonging larval life for greater dispersal, and others have actually shortened larval life for recruitment to limited habitats (Amaoka, 1979; Moser, 1981). There are several implications in this hypothesis that are relevant here: (1) There is some size range for transformation that is plesiomorphic for the order. This is usually implied to be ca. 10–25 mm because most pleuronectiforms metamorphose in this range. (2) Metamorphosis at markedly smaller (e.g., Achirinae) or larger (e.g., Bothidae, some pleuronectines) sizes are derived states. (3) According to the Regan-Norman model, prolonged larval development must have developed independently in several lines. Although metamorphosis at large sizes is most common in bothids, it is also known for some Pleuronectinae, the Poecilopsettinae, some species of the *Cyclopsetta* group, and some cynoglossids.

Size at metamorphosis is an important character for larval identification, but its use for inferring phylogenetic relationships in most instances is premature. Exceptions may exist in the Bothidae, where the extremely long premetamorphic lengths exhibited by some genera are probably apomorphic within the family and can be used for phylogenetic information.

Relative time of caudal-fin formation.—In most known larvae of flatfishes and other teleosts, formation of the caudal fin precedes or occurs with that of the dorsal and anal fins. The only exceptions known in pleuronectiforms are the cynoglossids. In this family, the caudal fin does not develop until the dorsal and anal fins are nearly completely developed. This pattern of development is considered apomorphic in pleuronectiforms.

Eye migration and dorsal-fin position at metamorphosis.—Eye migration has been observed in some flatfish groups. In the Psettodidae, Pleuronectinae, Paralichthyidae (excluding the *Cyclopsetta* group), Scophthalmidae, and apparently some Soleidae, the first ray of the dorsal fin is above or posterior to the eyes. At metamorphosis, the migrating eye crosses anterior to the dorsal-fin origin. These types of eye migration and dorsal-fin position appear to be plesiomorphic for the order. Several derived states for these characters occur. In at least one species of cynoglossid, a fleshy rostral beak is formed anterior to the dorsal-fin origin. Eye migration takes place between the rostral beak and the interorbital region. In some soleids, the dorsal-fin origin projects above the snout and the eye migrates between this projection and the neurocranium. In the Bothidae, the dorsal fin is anterior to the eye and attached to the ethmoid region. During migration, the eye goes between the base of the dorsal fin and the ethmoid region. A path for the migrating eye is created by detachment of the anterior section of the dorsal fin from the ethmoid region so that a narrow slit is formed, or some tissue in the path of the migrating eye is absorbed. A very similar type of eye migration occurs in some species of the *Cyclopsetta* group. However, in other members of this group, the eye migrates around the dorsal-fin origin (Gutherz, 1970; Tucker, 1982).

Phylogenetic information provided by larval characters

Although larvae of some critical groups are unknown or poorly known, some comments about phylogenetic relationships can be made in regard to groups where our knowledge is on a higher level.

Bothoids.—Spines in the otic or frontal regions of the neurocranium which are isolated or in small clusters appear to be limited to various groups of bothoids. If these spines prove to be homologous between these groups, they may be apomorphic within the order. In this interpretation, they would be primitive for bothoids and lost in various lines.

Paralichthyidae.—As discussed in the section on adult characters, this family as currently interpreted is polyphyletic due to the inclusion of *Tephrinectes* and *Thysanopsetta.* We do not consider these genera bothoids as defined by the caudal-fin complex. Their larvae are unknown.

We have interpreted the *Cyclopsetta* group as monophyletic based on some adult character states which are probably apomorphic. Although larvae of this group show certain states which appear to be apomorphic within bothoids (e.g., elongated left ventral-fin rays), not all species in this group show these.

The *Pseudorhombus* group is possibly definable by adult synapomorphies. In larvae of this group, we see no character states that are presently interpretable with certainty as synapomorphies.

In examining adult characters of the *Paralichthys* group, it appeared likely that this group had no synapomorphies. Larvae tend to support this. They show the following character states which appear to be plesiomorphic for the order: (1) presence of preopercular spines; (2) origin of the dorsal fin behind the eyes; (3) metamorphosis in a size range of 7.5–14.2 mm; and (4) eye migration anterior to the dorsal fin. In addition, at least some species show the following states which may prove to be plesiomorphic at least within the bothoids: (1) four or five elongated, early-forming dorsal-fin rays; and (2) presence of otic spines.

Bothidae.—With the exclusion of *Mancopsetta* and inclusion of *Perissias,* this family is definable by adult synapomorphies. Larvae of the Bothidae are probably better known than for any other family of flatfishes. However, larvae of many genera are still unknown (i.e., *Parabothus, Asterorhombus, Tosarhombus, Neolaeops, Japonolaeops,* and *Perissias*). Amaoka (1979) reviewed larval characters of most genera for which larvae are known. Known bothid larvae show the following character states which are interpreted as synapomorphies: (1) metamorphosis at a relatively large size (ca. 15–120 mm); (2) eye migration below the dorsal fin; (3) dorsal-fin origin anterior to eyes just prior to metamorphosis; (4) elongated, early-forming second dorsal-fin ray; and (5) lack of preopercular spines.

Larvae of some bothid genera have various combinations of otic-region, urohyal, cleithral, and basipterygial spines. It is tempting to use the presence of these spines to define bothid groups, and therefore, assume that they are apomorphic within the family. Spines in the otic region within the Bothidae are limited to the Taeniopsettinae as presently defined. However, spines in this region occur in other bothoid groups. Although sufficient comparative osteological work has not been done to show that these spines are homologous between taeniopsettines and other bothoids, use of these spines to infer close relationships between *Engyophrys, Taeniopsetta,* and *Trichopsetta* is questionable. Urohyal, cleithral, and basipterygial spines are known only from larvae of nine bothid genera. They occur in various combinations inter- and intragenerically. Amaoka (1969) presented a model of intergeneric relationships for Japanese bothids based on adult characters. Occurrence of these larval spines is scattered among the bothid lines hypothesized by Amaoka. This could indicate two possibilities: (1) the spines are apomorphic within the family, and Amaoka's model is incorrect; or (2) Amaoka's model is correct and the spines are plesiomorphic within the family and have been lost in several lines. Two major problems exist with Amaoka's phylogeny based on adult characters; it was constructed using eclectic methods and it did not include all genera. Interpretation of urohyal, basipterygial, and cleithral spines should await a cladistic analysis of bothid interrelationships based on adult characters.

Pleuronectidae.—Based on adult characters, we interpret this family as polyphyletic. Larvae of the four non-bothoid subfamilies are poorly known, and hence, of little aid in determining relationships of these groups. However, there are certain similarities in general body morphology between the few known samarine and poecilopsettine larvae. In regard to the Pleuronectinae, many adult states that are shared are plesiomorphic for pleuronectiforms or bothoids. This also appears to be true for most larval characters. The position of the dorsal-fin origin (posterior to the eyes) and the type of eye migration (anterior to the dorsal-fin origin) are plesiomorphic for the order. Some pleuronectine larvae have preopercular spines, which again, are probably plesiomorphic for flatfishes. Some genera show spines in the otic region of the neurocranium; these are possibly plesiomorphic for bothoids. All known pleuronectine larvae lack elongated dorsal-fin rays. However, this state is not limited to this group and a phylogenetic interpretation of it would be premature. In short, at present, we know of no character states that are unique to pleuronectine larvae or that can confidently be interpreted as apomorphic.

Egg characters

Except in certain groups, eggs of flatfishes are still too poorly known to be of much value in phylogenetic studies. One character of pleuronectiform eggs was used by Regan (1910) and Norman (1934) to interpret phylogeny, the presence of one oil globule in bothid eggs to separate them from those of pleuronectids which lack oil globules. We now have more information about the occurrence of oil globules in flatfish eggs, and the distribution of these character states is not exactly that predicted by the Regan-Norman model (preceding article, this volume). The obvious pattern here is that bothoids have 0–1 and soleoids, rhombosoleines, and *Mancopsetta* multiple oil globules. There are published exceptions to this. Watson and Leis (1974) identified three types of eggs with multiple oil globules as those of bothids. However, these authors expressed some doubt about the identifications of at least two of these egg types. These eggs are probably some other group (poecilopsettines or samarines?). Brownell (1979) identified some eggs which lacked oil globules as the soleid *Heteromycteris capensis*. This is the only soleid we are aware of that lacks multiple oil globules.

It is probably premature to use the oil-globule character for phylogenetic information until eggs from other groups are known. However, it is interesting and possibly significant that the soleoids, rhombosoleines, and *Mancopsetta* are so sharply separable from the bothoids in this character. One oil globule appears to be the most common state in the eggs of percomorph fishes (based on accounts in Watson and Leis, 1974; Russell, 1976; Fritzsche, 1978; Hardy, 1978b; Johnson, 1978; and Brownell, 1979). This may indicate that this state is plesiomorphic for pleuronectiforms. Corollaries of this would be that oil globules were lost in most pleuronectines, and multiple oil globules developed in a line leading to the soleoids, rhombosoleines, and *Mancopsetta*.

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U.S. Tuna Trade Summary, 1983

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Introduction

The year 1983 showed some signs of a turnaround for the U.S. tuna industry, which experienced a substantial decline in canned tuna sales, cannery receipts[1] of domestically caught and imported raw tuna, and domestic production activity during most of 1982. By the end of 1983, there was overall improvement in U.S. canned tuna sales, deliveries of raw tuna to U.S. canneries, and domestic processing activity.

Buoyed by a recovering U.S. economy and declining shelf prices, overall volume of canned tuna sales at the retail level was reported to have increased 7 percent for all of 1983. Improved retail sales acted to reduce the buildup of canned inventories that plagued the industry in 1982, and stimulated the flow of raw tuna through U.S. canneries. Cannery receipts of imported and domestically caught albacore, *Thunnus alalunga*, and tropical tunas (skipjack tuna, *Euthynnus pelamis*; yellowfin tuna, *T. albacares*; blackfin tuna, *T. atlanticus*; bluefin tuna, *T. thynnus*; and bigeye tuna, *T. obesus*) were up 6 percent from 1982, but were still 11 percent below the 5-year (1978-82) average volume of annual cannery receipts (Table 1). Despite fierce competition from foreign processors and record levels of canned tuna imports, overall canned tuna production rose 5 percent during 1983, though it was still 9 percent below the 1978-82 annual average (Table 1). These improvements in overall performance accompanied significant changes in the structures and operations of the U.S. tuna industry. These changes gained attention in 1982 and were heightened during 1983.

Table 1.—U.S. tuna cannery receipts and U.S. cannery production, 1982-83.

Item	Domestically caught 1982	Domestically caught 1983	Domestically caught % Chg.	Imports 1982	Imports 1983	Imports % chg.	Total 1982	Total 1983	Total % Chg.	Average 1978-82	Average % Chg.
Cannery receipts[1]	228,156	285,554	+25	272,490	246,495	−9	500,646	532,049	+6	600,307	−11
Total pack[2]							27,088	28,382	+5	31,278	−9

[1]In short tons: Includes imports and domestically caught tuna.
[2]Thousands of standard cases. A standard case consists of 48 6.5-ounce cans of light meat tuna and 48 7-ounce cans of albacore or white meat tuna.
Source: Statistics and Market News, Southwest Region, NMFS, NOAA.

Due in part to the adverse effects of El Niño on tuna resources in the eastern Pacific Ocean[2] and continuing problems of access to traditional fishing grounds in this area, as well as the attraction of potentially more abundant tuna resources in the western Pacific Ocean, the movement of U.S. tuna purse seiners to the western Pacific accelerated during 1983. At least 60 of the 127 seiners comprising the U.S. tuna purse seine fleet operated in the western Pacific during 1983. U.S. seiners fishing in this area were quite successful, with regard to volume of catch, and for the first time, cannery receipts of domestically caught tuna from this area accounted for the greatest share of domestically caught cannery receipts by oceanic area: 171,153 short tons (tons), 60 percent of total domestically caught cannery receipts for 1983 (Table 2). Nevertheless, a significant portion of the U.S. tuna fleet—about 25 percent—was inactive all or part of 1983 for economical reasons. U.S. canneries continued to sell, or attempted to sell, interests they held in tuna purse seiners, reflecting the likelihood that tuna fishing under current conditions is more efficient or cost-effective when undertaken by independent vessels.

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[1] Cannery receipts include only tuna destined for U.S. canneries. They exclude U.S.-caught tuna landed at foreign sites or U.S.-caught tuna landed at U.S. sites that is destined for foreign canneries, U.S.-caught tuna destined for the fresh-fish market; they also exclude tuna imported as flakes, imported tuna not fit for human consumption, and imported "sushi" grade tuna.

[2] The eastern and western Pacific are distinguished at long. 150° W.

Table 2.—U.S. tuna cannery receipts (short tons) by receiving site and ocean of origin, 1982-83.

Item	Domestically caught			Imports			Total		
	1982	1983	% Chg.	1982	1983	% Chg.	1982	1983	% Chg.
Site									
California	140,850	134,658	− 4	56,397	51,481	− 9	197,247	186,139	− 6
Am. Samoa/Hi	42,388	79,240	+ 87	41,180	35,983	− 13	83,568	115,223	+ 38
Puerto Rico	44,918	71,656	+ 60	174,913	159,031	− 9	219,831	230,687	+ 5
Total	228,156	285,554	+ 25	272,490	246,495	− 10	500,646	532,049	+ 6
Ocean									
Eastern Atlantic		21	+ 100	78,552	55,911	− 29	78,552	55,932	− 29
Western Atlantic	115	77	− 33	41,306	40,643	− 2	41,421	40,720	− 2
Eastern Pacific	159,618	115,303	− 28	31,164	12,237	− 61	190,782	127,540	− 33
Western Pacific	68,423	170,153	+ 149	102,086	118,663	+ 16	170,509	288,816	+ 69
Indian				19,382	19,041	− 2	19,382	19,041	− 2
Total	228,156	285,554	+ 25	272,490	246,495	− 10	500,646	532,049	+ 6

Source: Statistics and Market News, Southwest Region, NMFS, NOAA.

Table 3.—U.S. albacore cannery receipts and U.S. white meat cannery production, 1982-83.

Item	1982	1983	% Chg.	1978-82	% Chg.
Total cannery receipts[1]	101,564	83,325	− 18	103,815	− 20
Total pack[2]	6,021	5,105	− 15	6,056	− 16

[1] In short tons: Includes imports and domestically caught tuna.

[2] Thousands of standard cases. A standard case consists of 48 7-ounce cans of white meat tuna.

Source: Statistics and Market News, Southwest Region, NMFS, NOAA.

Table 4.—U.S. albacore cannery receipts (short tons) by receiving site, 1982-83.

Site	Domestically caught			Imports			Total		
	1982	1983	% Change	1982	1983	% Change	1982	1983	% Change
Continental	5,099	9,434	+ 85	11,115	5,616	− 49	16,214	15,050	− 7
Am. Samoa/HI	1,866	1,032	− 45	22,814	17,134	− 25	24,680	18,166	− 26
Puerto Rico	0	4	+ 100	60,670	50,105	− 17	60,670	50,109	− 17
Total	6,965	10,470	+ 50	94,599	72,855	− 23	101,564	83,325	− 18

Source: Statistics and Market News, Southwest Region, NMFS, NOAA.

More than 75 percent of the domestically caught tuna from the western Pacific was delivered or transshipped to offshore canneries located in American Somoa, Hawaii, and Puerto Rico in 1983. That offshore processing sites are becoming more dominant in terms of U.S. tuna production is also reflected in the fact that in 1983, about 63 percent of the total U.S. pack of canned tuna was processed at offshore facilities. This compares with 61 percent of total production at offshore sites in 1982 and 58 percent in 1981. As a result of this continuing shift in canned production to offshore sites, employment at California canneries, which fell sharply in 1982, is reported to have decreased further during 1983, by the equivalent of about 1,250 full-time jobs.

In the sections that follow, information pertaining to the production of raw and processed tuna by the U.S. tuna industry during 1983, and the consumption of tuna products by U.S. consumers is reviewed in more detail. In the last section, several issues and events are discussed that affected the industry's performance during 1983.

U.S. Production of Albacore (White Meat Tuna)

While overall improvement in the performance of the U.S. tuna industry was observed in 1983, this was not entirely the case when production and consumption are distinguished by fishery and product category. According to industry reports, consumption of canned white meat tuna, which is 100 percent albacore, increased almost 17 percent in 1983. On the other hand, total cannery receipts, 83,325 tons, and canned production of albacore, 5,105 thousand standard cases, were down 18 and 15 percent, respectively, for 1983 (Table 3). The fact that cannery deliveries and domestic production declined while sales showed an increase in 1983 probably reflects either a move to reduce canned white meat inventories on the part of processors or dominance of U.S. retail sales by imported canned white meat tuna, or both. In any case, retail sales were stimulated through significant albacore price adjustments at the ex-vessel, wholesale, and retail levels.

U.S. 1983 Cannery Receipts of Domestically Caught Albacore

In recent years the U.S. albacore fishery has had upwards of 750 vessels participating on a regular basis. The majority of these vessels are in the 40-to 50-foot length range and use troll gear exclusively. There is also a number of larger baitboats that operate in the fishery, and more recently several vessels have started to fish albacore using drift gillnets. Many of the vessels are of a multipurpose design, capable of fishing albacore using a variety of gears, as well as operating in a number of alternative fisheries (e.g., ocean salmon, crab, tropical tuna).

The U.S. albacore fishery occurs almost entirely in the Pacific Ocean north of the Equator and seaward from the west coast to about long. 180°. In 1983 all cannery receipts of domestically caught tuna, 10,470 tons, came from this area with the exception of 4 tons which came from the Atlantic Ocean. Cannery receipts of domestically caught albacore for 1983 were up 50 percent from 1982 (Table 4). This significant increase can largely be attributed to a combination of environmental and economic factors.

Albacore ex-vessel prices, which fell sharply in 1982, continued to decline in 1983. Early in the season a two-tiered price system paid fishermen $1,250 per ton (not adjusted for fish quality) for albacore 9 pounds and over and $975 per ton for albacore less than 9 pounds, a decrease of 12 and 32 percent, respectively, from 1982. These price reductions meant that fishermen would have to experience substantially greater success on the fishing grounds if they were to improve their collective economic performance from 1982. Such was the case, for the unusual warming of nearshore waters brought about by El Niño increased the availability of albacore to U.S. fishermen operating along the west coast.

However, while the effects of El Niño benefited the coastal albacore fishery, they tended to have an unfavorable impact on the offshore and mid-Pacific albacore fisheries. This is partly revealed in the 33 percent decline in cannery receipts of domestically caught and imported albacore from the western Pacific during 1983 (Table 5). Because of these factors, there was a ready market for relatively less expensive U.S.-caught albacore in 1983 which generated $13 million in ex-vessel revenue, up 35 percent from 1982. Dividing 1983 albacore ex-vessel revenue by total cannery receipts yields a weighted ex-vessel price of $1,248 per ton, down 10 percent from 1982.

Table 5.—U.S. albacore cannery receipts (short tons) by ocean of origin, 1982-83.

Ocean	Domestically caught 1982	Domestically caught 1983	Domestically caught % Chg.	Imports 1982	Imports 1983	Imports % Chg.	Total 1982	Total 1983	Total % Chg.
Eastern Atlantic	0	0	0	19,815	16,935	− 15	19,815	16,935	− 15
Western Atlantic	0	4	+ 100	21,129	16,127	− 24	21,129	16,131	− 24
Eastern Pacific	5,099	9,434	+ 85	48	243	+ 400	5,147	9,677	+ 88
Western Pacific	1,866	1,032	− 45	36,760	24,783	− 33	38,626	25,815	− 33
Indian	0	0	0	16,847	14,767	− 12	16,842	14,767	− 12
Total	6,965	10,470	+ 50	94,599	72,855	− 23	101,564	83,324	− 18

Source: Statistics and Market News, Southwest Region, NMFS, NOAA.

Table 6.—Preliminary U.S. Imports as received (short tons) of fresh, frozen, and partially processed whole tuna by exporting country for the 10 leading exporters during 1982-83.

Source	Albacore 1982	Albacore 1983	Skipjack tuna 1982	Skipjack tuna 1983	Yellowfin tuna[1] 1982	Yellowfin tuna[1] 1983	Unident. tuna 1982	Unident. tuna 1983	Total 1982	Total 1983	Total % Chg.
Panama			10,321	4,728	12,683	7,218	910	501	23,914	12,447	− 48
Venezuela			5,482	5,647	4,742	4,134	375	535	10,599	10,316	− 3
Brazil	609	619	14,539	13,996	416	293	3	4	15,567	14,912	− 4
France	2,738	794	18,784	13,365	4,570	4,133	166	59	26,258	18,621	− 29
Singapore	1,990	2,114	2,555	3,281	353	205	63		4,961	5,600	+ 13
Philipp.	360	50	5,436	5,140	2,077	1,579	2	1	7,875	6,770	− 14
Rep. Korea	1,905	2,705	3,709	8,802	884	2,067	643	207	7,141	13,781	+ 93
Taiwan	27,434	17,829	2,062	3,842	767	1,976	36	41	30,299	23,688	− 22
Japan	21,308	22,826	19,412	29,450	2,902	844	55	26	43,677	53,146	+ 22
Ghana			13,602	22,198	1,066	1,162	41	53	14,709	23,413	+ 59
"Other"	37,349	25,224	35,900	29,750	20,151	13,948	872	973	94,272	69,895	− 26
Total[2]	93,693	72,161	131,802	140,469	50,611	37,559	3,166	2,400	279,272	252,589	− 10

[1] Includes bigeye and bluefin tuna.

[2] Individual species totals may not agree with those reported elsewhere due to unidentified category. Overall totals may not agree with those reported elsewhere because they can include tuna not destined for U.S. canneries and exclude foreign transshipments.

U.S. 1983 Production of Canned White Meat Tuna

Albacore is consumed almost exclusively as canned white meat tuna by U.S. consumers. Traditionally, the most popular albacore product has been the 7-ounce (standard size) can of solid white meat tuna packed in water.

San Diego and San Pedro, Calif., Mayaguez and Ponce, Puerto Rico, Honolulu, Hawaii, and Pago Pago, American Samoa, are the major U.S. tuna receiving and processing sites. For reporting purposes, tuna receipts are combined for California and for American Samoa and Hawaii (American Samoa/Hawaii). Of the total 1983 raw (whole and other than whole) albacore cannery supply (83,325 tons), 60 percent was delivered to Puerto Rico, 22 percent to American Samoa/Hawaii, and the remaining 18 percent to California. All three areas showed declines in total albacore receipts, 17, 26, and 7 percent, respectively, from 1982 (Table 4).

Of the total 1983 domestically caught, raw albacore cannery receipts, 90 percent was received in California. Virtually all of the remainder was received at American Samoa/Hawaii sites except for 4 tons delivered to Puerto Rico. Domestically caught albacore delivered to California rose 85 percent from 1982 to 1983, while receipts at American Samoa/Hawaii sites decreased 45 percent. There was no domestically caught albacore tuna delivered to Puerto Rico in 1982 (Table 4).

U.S. cannery receipts of imported raw albacore totaled 72,855 tons in 1983, down 23 percent from 1982. Imports composed 87 percent of the total 1983 cannery supply of albacore compared with 93 percent in 1982. Puerto Rico was the major receiving site for U.S. imports of raw albacore during 1983, with 50,105 tons or 69 percent of the total. American Samoa/Hawaii followed with 24 percent of the 1983 total, and California accounted for the remaining 7 percent. Albacore imports received in Puerto Rico during 1983 decreased 17 percent from 1982, while imports received at American Samoa/Hawaii and California declined 25 and 49 percent, respectively, from 1982 (Table 4).

Japan was the leading exporter of raw albacore to U.S. canneries during 1983 with about 22,826 tons or 31 percent of the total raw albacore imports. Taiwan was next with 17,829 tons, 24 percent of the total (Table 6).

Table 7.—U.S. production of canned tuna (thousand standard cases) by processing site, 1982-83.

	White meat			Light meat			Total		
Site	1982	1983	% Change	1982	1983	% Change	1982	1983	% Change
California	954.4	781.1	– 18	9,427.4	9,190.5	– 3	10,197.4	9,971.5	– 2
American Samoa/HI	1,537.2	911.9	– 41	3,004.2	5,482.3	+ 82	4,541.5	6,394.3	+ 41
Puerto Rico	3,529.1	3,412.2	– 3	8,635.1	8,604.1		12,164.2	12,016.3	– 1
Total	6,020.7	5,105.2	– 15	21,066.7	23,276.9	+ 11	27,087.4	28,382.1	+ 5

Source: Statistics and Market News, Southwest Region, NMFS, NOAA.

Table 8.—U.S. tropical tuna cannery receipts and U.S. light meat cannery production, 1982-83

Item	1982	1983	% Chg.	1978-82	% Chg.
Total cannery receipts[1]	399,082	448,724	+ 12	496,492	– 10
Total pack[2]	21,067	23,277	+ 10	25,222	– 7

[1] In short tons: Includes imports and domestically caught tuna.
[2] Thousands of standard cases. A standard case consists of 48 6.5-ounce cans of white meat tuna.
Source: Statistics and Market News, Southwest Region, NMFS, NOAA.

Raw albacore imports received at U.S. canneries in 1983 were valued at about $97 million, down almost 45 percent from 1982. Dividing this value by the corresponding volume results in a weighted average import price of $1,335 per ton for raw albacore in 1983, almost 28 percent below that for 1982.

In 1983, the Pacific Ocean provided 43 percent of the total U.S. cannery supply of albacore. The Atlantic and Indian Oceans followed with 40 and 17 percent, respectively, of the total supply, almost all imports. This pattern was unchanged from 1982. Because of the significant increase in domestically caught albacore cannery receipts, the eastern Pacific was the only oceanic area from which an increase in supply (88 percent) was reported in 1983 (Table 5).

Of the three major U.S. canned tuna production centers, Puerto Rico was the primary U.S. albacore processing site during 1983 with 3,412,000 standard cases, 67 percent of the total white meat pack for 1983. This is a 3 percent decrease from 1982. American Samoa/Hawaii followed with 912,000 standard cases, 18 percent of the total 1983 white meat pack, down 41 percent from 1982. Continental sites produced 781,000 standard cases of white meat tuna in 1983, 15 percent of the total, and an 18 percent decrease from 1982 (Table 7).

Wholesale list prices for U.S. produced, advertised white meat tuna ranged from $59.45 to $62.50 per standard case at the beginning of 1983 and fell to $53.17-60.63 per standard case by year's end, a decline of between 11 and 3 percent. Also, discounts further reduced the price to as low as $40.20 for a standard case. In terms of total value, U.S. production of canned white meat tuna—advertised and private brands—generated $196 million in 1983, down 29 percent from 1982. Based on total white meat volume, the weighted average price was $38.40 per standard case compared with $45.74 for 1982, a 16 percent decrease.

U.S. Production of Tropical Light Meat Tuna

U.S. tuna industry performance in terms of tropical or light meat tuna harvesting and production improved substantially in 1983. Consumption of canned light meat tuna reportedly rose 12 percent during 1983. There was a similar increase in total (U.S.-caught and imported) cannery receipts of tropical tunas, to 448,724 tons in 1983. However, the volume of 1983 tropical tuna cannery receipts was still 10 percent below the 1978-82, 5-year average (Table 8). Production of canned light meat tuna rose in 1983, to a total pack of 23,277,000 standard cases, which was up 10 percent from 1982 (Table 8). Declining prices at the ex-vessel, wholesale, and retail levels during 1982 and most of 1983 led to increased purchases of tropical tuna by both producers and consumers.

U.S. 1983 Cannery Receipts of Domestically Caught Tropical Tunas

In 1983, the U.S. tropical tuna fleet consisted of 146 vessels: 127 purse seiners and 19 bait boats (pole and line gear). This compares with a total fleet of 139 vessels in 1982: 127 purse seiners and 12 baitboats. Fleet carrying capacity was 129,126 tons in 1983, up 2 percent from 1982. However, by the end of 1983, there were about 30 inactive purse seiners in the U.S. tropical tuna fleet. Purse seiners account for by far the bulk of domestically caught tropical tuna cannery receipts, over 97 percent in 1983.

In 1983, domestically caught cannery receipts of tropical tunas were 275,084 tons, 24 percent above 1982 (Table 9). Practically all of this was taken from the Pacific Ocean. However, in 1983 more vessels, representing a disproportionately greater amount of carrying capacity, operated in the western Pacific than in the historically more popular eastern Pacific Ocean. U.S. vessels active in the western Pacific numbered 60 during 1983, an increase of 85 percent from 1982, while 57 vessels were active in the eastern Pacific, a 40 percent decrease from 1982. Carrying capacity of the vessels operating in the western Pacific was 73,395 tons in 1983, an average of 1,223 tons per vessel, compared with 30,986 tons, or an average of 544 tons per vessel, for the eastern Pacific. Fifty-nine of the vessels that operated in the western Pacific had carrying capacities of at least 1,000 tons as opposed to only 15 of the vessels operating in the eastern Pacific. Very little U.S. tropical tuna fishing occurred in the Atlantic Ocean during 1983.

Ex-vessel prices for domestically caught tropical tuna continued to fall during 1983. At the close of 1983, the posted ex-vessel price (without quality adjustments) in effect for skipjack tuna in the 3.0-4.0 pound range was $640 per ton, down 9 percent from the close of 1982. The posted ex-vessel price for yellowfin tuna in the 7.5-20.0 pound range (without quality adjustments) at the end of 1983 was $990 per ton, 6 percent below that at the close of 1982. The full range of skipjack and yellowfin tuna ex-vessel prices for 1983 is shown in Table 10.

Domestically caught skipjack tuna cannery receipts totaled 155,040 tons for 1983, up significantly, 51 percent, from 1982 (Table 11). Domestically caught skipjack tuna receipts were valued at $124 million ex-vessel in 1983, a 26 percent increase over 1982. This yields a weighted ex-vessel skipjack tuna price of $800 per ton for 1983, down 16 percent from 1982. Cannery receipts of domestically caught yellowfin tuna (includes bigeye, bluefin, and blackfin tuna) totaled 120,044 tons in 1983, up slightly, 1 percent, from 1982 (Table 11). Domestic deliveries of yellowfin tuna generated about $124 million in ex-vessel revenues during 1983, 7 percent below 1982. The weighted ex-vessel price for yellowfin tuna in 1983 was $1,031 per ton, a decrease of 8 percent from 1982. Total ex-vessel revenues from domestically caught tropical tuna receipts were about $248 million in 1983. This is a 7 percent increase over 1982, indicating that U.S. tropical tuna fishermen more than offset the loss in per unit revenue through increased cannery deliveries.

U.S. Production of Canned Light Meat Tuna

Skipjack and yellowfin tuna are blended together and canned as light meat tuna, the most popular tuna product consumed in the United States. The 6.5-ounce (standard size) can of chunk style, light meat tuna in water led light meat tuna sales in 1983.

Table 9.—U.S. tropical tuna cannery receipts (short tons) by ocean of origin, 1982-83.

Ocean and Species	Domestically caught 1982	Domestically caught 1983	Domestically caught % Chg.	Imports 1982	Imports 1983	Imports % Chg.	Total supply 1982	Total supply 1983	Total supply % Chg.
Skipjack tuna									
Eastern Atlantic		21	+ 100	49,417	34,358	− 30	49,417	34,379	− 30
Western Atlantic		3	+ 100	17,119	18,070	+ 6	17,119	18,073	+ 6
Eastern Pacific	59,925	40,103	− 33	11,916	4,502	− 62	71,841	44,605	− 38
Western Pacific	42,529	114,913	+ 182	46,892	75,066	+ 60	89,421	189,979	+ 112
Indian				1,763	3,312	+ 88	1,763	3,312	+ 88
Subtotal	102,454	155,040	+ 51	127,107	135,308	+ 6	229,561	290,348	+ 26
Yellowfin tuna[1]									
Eastern Atlantic				9,320	4,618	− 50	9,320	4,618	− 50
Western Atlantic	115	70	− 39	3,058	6,446	+ 111	3,173	6,516	+ 105
Eastern Pacific	94,594	65,766	− 30	19,200	7,492	− 61	113,794	73,258	− 36
Western Pacific	24,028	54,208	+ 126	18,434	18,814	+ 2	42,462	56,092	+ 32
Indian				772	962	+ 25	772	962	+ 25
Subtotal	118,737						69,521	158,376	− 7
Total tropical tuna									
Eastern Atlantic		21	+ 100	58,737	38,976	− 34	58,737	38,997	− 34
Western Atlantic	115	73	− 37	20,177	24,516	+ 22	20,292	24,584	+ 21
Eastern Pacific	154,519	105,869	− 31	31,116	11,994	− 61	185,635	117,863	− 37
Western Pacific	66,557	169,121	+ 154	65,326	93,880	+ 44	131,883	263,001	+ 99
Indian				2,535	4,274	+ 69	2,535	4,274	+ 69
Grand total	221,191	275,084	+ 24	177,891	173,640	− 2	399,082	448,724	+ 12

[1] Includes bigeye, bluefin, and blackfin tuna.
Source: Statistics and Market News, Southwest Region, NMFS, NOAA.

Table 10.—Posted ex-vessel prices ($/ton), without quality adjustments, for skipjack and yellowfin tuna (includes bigeye, bluefin, and blackfin tuna), 1982-83.

Size (lb)	Skipjack tuna 1982	Skipjack tuna 1983	Skipjack tuna % chg.	Yellowfin tuna 1982	Yellowfin tuna 1983	Yellowfin tuna % chg.
<3.0	$500	$400-440	− 16	$890	$400	− 55
3.0-4.0	$700	$640	− 9	$890	$640	- 28
>4.0, < =7.5	$890	$800	− 10	$890	$800	- 10
>7.5	$890	$900	+ 1			
>7.5, < =20.0				$1,050	$990	− 6
>20.0				$1,170	$1,125	− 4

Source: Statistics and Market News, Southwest Region, NMFS, NOAA.

Table 11.—U.S. tropical tuna cannery receipts (short tons) by receiving site, 1982-83.

Species and site	Domestically caught 1982	Domestically caught 1983	Domestically caught % Chg.	Imports 1982	Imports 1983	Imports % Chg.	Total supply 1982	Total supply 1983	Total supply % Chg.
Skipjack tuna									
California	56,167	58,521	+ 4	37,108	41,450	+ 12	93,275	99,971	+ 7
Am Samoa/HI	26,598	54,911	+ 106	8,729	9,182	− 5	35,327	64,093	+ 81
Puerto Rico	19,689	41,608	+ 111	81,270	84,676	+ 4	100,959	126,284	+ 25
Subtotal	102,454	155,040	+ 51	127,107	135,308	+ 6	229,561	290,348	+ 26
Yellowfin tuna[1]									
California	79,584	66,703	− 16	8,174	4,415	− 46	87,758	71,118	− 19
Am. Samoa/HI	13,924	23,297	+ 67	9,637	9,667		23,561	32,964	+ 40
Puerto Rico	25,229	30,044	+ 14	32,973	24,250	− 25	58,202	54,299	− 7
Subtotal	118,737	120,044	+ 1	50,784	38,332	− 25	169,521	158,376	− 7
Total tropical tuna									
California	135,751	125,224	− 8	45,282	45,865	+ 1	181,033	171,089	− 5
Am. Samoa/HI	40,522	78,208	+ 93	18,366	18,849	+ 3	58,888	97,057	+ 65
Puerto Rico	44,918	71,652	+ 60	114,243	108,926	− 5	159,161	180,551	+ 13
Grand total	221,191	275,084	+ 24	177,891	173,640	− 2	399,082	448,724	+ 12

[1] Includes bigeye, bluefin, and blackfin tuna.
Source: Statistics and Market News, Southwest Region, NMFS, NOAA

The total supply of raw tropical tuna, 448,724 tons, was delivered to canneries in Puerto Rico, American Samoa and Hawaii, and California during 1983. Puerto Rico was the leading receiving site in 1983 with 180,551 tons, 40 percent of the total cannery supply. California canneries followed with 38 percent of the total supply and American Samoa/Hawaii sites received 22 percent of the total 1983 supply. Total tropical tuna receipts for Puerto Rico increased 13 percent from 1982, increased 65 percent for American Samoa/Hawaii, but fell 5 percent for California (Table 11).

Of the total domestically caught receipts of tropical tuna for 1983, 125,224 tons (46 percent) was received in California, 78,208 tons (28 percent) at American Samoa/Hawaii sites, and the remaining 71,652 tons (26 percent) in Puerto Rico. Domestically caught deliveries of tropical tuna to California fell 8 percent from 1982 but increased 93 percent in American Samoa/Hawaii and increased 60 percent in Puerto Rico. Skipjack tuna dominated domestically caught tropical tuna receipts, composing 56 percent of the total domestically caught tropical tuna receipts for 1983 (Table 11).

Imported tropical tuna receipts totaled 173,640 tons in 1983, 2 percent below 1982. Imports made up 39 percent of the total tropical tuna cannery supply in 1983 vs. 45 percent in 1982. Puerto Rico was the major receiving site for tropical tuna imports during 1983 with 108,926 tons, 63 percent of the total. California followed with 26 percent and American Samoa/Hawaii received the remaining 11 percent. Receipts of imported tropical tuna in Puerto Rico decreased 5 percent from 1982 and increased slightly for California and American Samoa/Hawaii sites (1 and 3 percent, respectively). Skipjack tuna was the major tropical tuna species imported during 1983, with 135,308 tons, comprising 78 percent of total tropical tuna imports. Yellowfin tuna contributed the balance. Overall skipjack tuna imports were up 6 percent from 1982, while yellowfin tuna imports fell 25 percent (Table 11).

The leading exporter of raw tropical tuna to the United States in 1983 was Japan, with approximately 30,320 tons or 12 percent of the 1983 total. Imports from Japan consisted of 97 percent skipjack tuna and the remainder yellowfin and unidentified tuna. Ghana followed with 23,413 tons, 9 percent of the total; of this 95 percent was skipjack tuna, and the rest was yellowfin and unidentified tuna (Table 6).

The total value of 1983 tropical tuna imports received at U.S. canneries was $138 million, down 21 percent from 1982. The value of skipjack tuna imports was approximately $100 million and the value of yellowfin tuna imports was about $38 million, decreases of 13 and 36 percent, respectively, from 1982. These values convert to weighted average prices of $742 per ton for skipjack tuna imports and $983 per ton for yellowfin tuna. This represents price decreases of 19 percent for skipjack tuna and 16 percent for yellowfin tuna from 1982.

The Pacific Ocean was the major source of U.S. tropical tuna cannery receipts. For all tropical tuna species combined, the Pacific provided 380,864 tons during 1983, 85 percent of the total supply. The Atlantic and Indian Oceans provided 14 and 1 percent, respectively, and virtually all were imports. On a regional basis, the western Pacific was the leading source of tropical tuna receipts contributing 263,001 tons, 59 percent of the total tropical tuna cannery supply in 1983. Total tropical tuna receipts from the western Pacific rose 99 percent from 1982. Of the total tropical tuna receipts originating in the western Pacific during 1983, 64 percent (169,121 tons), was domestically caught; the remainder (93,880 tons) consisted of imports. Domestically caught tropical tuna receipts from the western Pacific increased 154 percent from 1982 while imports increased 44 percent. Skipjack tuna dominated tropical tuna receipts from the western Pacific in 1983, contributing 72 percent of the total receipts from this oceanic area, and 42 percent of the total tropical tuna receipts from all areas. Other oceanic regions contributing to the 1983 U.S. cannery supply, in order of importance, were the eastern Pacific (primarily domestically caught yellowfin tuna), the eastern Atlantic (almost all skipjack tuna imports), and the western Atlantic (mainly skipjack tuna imports). A breakdown of the 1983 tropical tuna cannery supply by ocean of origin is presented in Table 9.

California was the leading U.S. production center for canned light meat tuna during 1983, with 9,190 thousand cases, 39 percent of the total light meat pack for 1983. Next was Puerto Rico with 8,604,000 standard cases, 37 percent of the total, followed by American Samoa/Hawaii with 5,482,000 standard cases, 24 percent of the 1983 total. Production of canned light meat tuna in California was down 3 percent from 1982, unchanged from 1982 in Puerto Rico, and up 82 percent from 1982 in American Samoa/Hawaii (Table 7).

The wholesale list price of U.S. produced advertised light meat tuna ranged from $43.00 to $46.65 a standard case, discounted to as low as $34.00 a standard case at the beginning of 1983. By the end of 1983 it had fallen to between $40.15 and $41.05 per standard case, a decrease of 7-12 percent. Total U.S. production of canned light meat tuna—both advertised and private label—in 1983 was valued at $625 million, down 3 percent from 1982. Dividing total value by total volume yields a weighted average price of $26.86 for a standard case of light meat tuna in 1983, down 12 percent from 1982.

Canned Tuna Imports

The United States imposes tariffs on canned tuna imports in two categories: Tuna in oil and tuna not in oil. The tariff schedules on imported canned tuna were originally established when light meat tuna packed in oil was much more popular among U.S. consumers than light meat not in oil. Since then, U.S. consumption has shifted significantly in favor of light meat tuna packed in water.

Canned tuna in oil is subject to a 35

Table 12.—Imports of canned tuna (in oil and not in oil) by exporting country and their corresponding value, 1978-83.

	Quantity (1,000 lb)						Value (1,000 dollars)					
Source	1978	1979	1980	1981	1982	1983	1978	1979	1980	1981	1982	1983
Japan	35,887	28,366	24,794	21,271	26,481	20,387	46,343	37,055	42,015	36,453	38,561	24,643
Philippines	3,374	6,998	13,777	21,451	27,631	32,018	3,536	7,319	20,043	30,504	31,085	32,291
Thailand	1,551	4,844	6,405	10,315	18,667	39,930	1,886	5,135	8,875	15,400	22,711	43,259
Taiwan	9,051	12,282	15,947	15,771	10,704	18,710	9,667	14,103	23,316	24,631	14,366	22,772
Australia	0	0	0	58	1,930	2,799				105	3,451	3,684
Malaysia	651	292	66	696	755	3,083	746	314	76	1,230	1,242	4,068
Indonesia	0	0	0	146	595	2,634				209	699	2,679
Maldives	0	62	600	592	327	0		67	825	874	379	
Spain	132	336	146	170	120	133	294	501	367	402	300	268
Singapore	0	0	28	65	120	329			38	91	141	386
All other	1,136	523	1,792	316	248	2,306	1,349	579	1,698	459	412	3,274
Total	51,781	53,704	63,553	70,852	87,579	122,329	63,822	65,071	97,254	110,358	113,347	137,324

Source: U.S. International Trade Commission, Publication 841, Summary of Trade and Tariff Information, July 1983, Bureau of Census.

percent ad valorem tariff and imports are negligible. Canned tuna imports not in oil are controlled under a tariff rate quota which allows imports up to 20 percent of the previous year's domestic production at one rate, with imports above this level subject to a higher rate. Prior to reaching the quota on canned tuna not in oil, imports of canned white meat tuna not in oil are distinguished from imports of canned light meat tuna not in oil. Once the quota is reached however, there is no distinction between light and white meat tuna.

In 1983 the tariff rate on tuna not in oil was 6 percent ad valorem below quota and 12.5 percent above quota. The 1983 quota on imports of canned tuna not in oil was 95,620,000 pounds or approximately 4,900,000 standard, light meat equivalent, cases. Total imports amounted to a record 122,329,000 pounds or almost 6,300,000 standard, light meat equivalent, cases, an increase of 40 percent from 1982. When the 1983 quota was reached, white meat comprised 16 percent of the canned imports not in oil, the remaining 84 percent was light meat tuna. U.S. imports of canned tuna in oil—virtually all light meat tuna—totaled 197,000 pounds in 1983 or about 10,102 standard cases, down 8 percent from 1982.

Thailand was the leading exporter of canned tuna to the United States in 1983 with 39,930,000 pounds of canned product or about 2,000,000 standard, light meat equivalent, cases. This was 33 percent of the total U.S. imports of canned tuna. The Philippines followed with 32,018,000 pounds, or about 1,600,000 standard, light meat equivalent, cases, representing 26 percent of the total 1983 canned imports.

The value of all imported canned tuna was approximately $137 million in 1983, an increase of 21 percent from 1982. This converts to a weighted average standard, light meat equivalent, case price of $21.89, which is 13 percent below that for 1982. Imports of canned tuna by exporting country and their corresponding value are shown in Table 12.

U.S. Consumption of Canned Tuna

U.S. civilian per capita consumption of canned tuna—both light and white meat—in 1983 was 3.0 pounds, 11 percent above 1982. Assuming that light meat comprises 80 percent of the total per capita consumption, and the remainder is white meat, domestic consumption is estimated to be 0.60 pounds of white meat tuna and 2.40 pounds of light meat tuna per capita for 1983, compared with 0.54 pounds and 2.16 pounds, respectively, for 1982. This is equivalent to 1.28 standard cans of white meat and 5.91 standard cans of light meat tuna per capita for 1983, and 1.15 standard cans of white meat and 5.32 standard cans of light meat tuna per capita for 1982. Based on the National Marine Fisheries Service's "Operation Price Watch," the 10-city average price for domestically produced canned tuna, U.S. consumers paid an average of $1.49 per can for white meat tuna and $0.87 per can for light meat tuna during 1983, a decrease of 3 percent and 9 percent, respectively, from 1982. This results in a slight increase in estimated per capita tuna expenditures: $7.05 for 1983 versus $6.88 for 1982. These estimates do not take into account domestic consumption of imported canned tuna.

Discussion

U.S. tuna industry performance during 1983 was highlighted by increased domestically caught cannery receipts of albacore and tropical tuna, an increase in the light meat tuna pack, and increased purchases of tuna products by U.S. consumers. However, marked improvement in these areas was not realized without some significant changes in the industry's structure and operations. Some of these changes can be traced back to the late 1970's and early 1980's when rising production costs, particularly for fuel, led to record high prices at the ex-vessel, wholesale, and retail levels. Higher prices increased consumer resistance to purchases of canned tuna resulting in an accumulation of canned tuna inventories. To stimulate consumption, the U.S. tuna industry initiated price reductions in mid-1981 and prices at all levels have declined since. This action, together with overall improvements in the U.S. economy during the past year, has enhanced canned tuna sales and done much toward restoring U.S. canned tuna production to its historic average.

To accommodate wholesale price reductions and improve their inventory positions, U.S. processors sought to streamline cannery operations. Production at California canneries was cut back severely beginning in 1982 with the closure of one major cannery and significant contractions in the remaining operations. Processing in California declined further in 1983 as major U.S. canners shifted their operations to offshore sites (Puerto Rico, American Samoa/ Hawaii) to take advantage of more favorable operating conditions.

Adverse conditions in the processing sector of the U.S. tuna industry at the end of 1981 filtered downward to U.S. tuna fishermen in the form of substantially lower ex-vessel tuna prices and difficulties and delays in selling their catches. Further, canneries were anxious to divest themselves of interests they held in tropical tuna vessels and to cut back their financial support to independently owned vessels. Under these circumstances many vessels were unable to participate in the fisheries. In addition to weakened ex-vessel markets, U.S. tropical tuna fishermen faced continued uncertainty in terms of access to traditional eastern Pacific fishing grounds, decreased availability of tropical tuna resources in the eastern Pacific attributed to El Niño, and increased competition from foreign fishermen. These factors, together with potentially more abundant tropical tuna resources to be found in the western Pacific Ocean, contributed to a reduction in the number of active U.S. tropical tuna vessels and a redeployment of most large U.S. purse seiners to the western Pacific in 1983. Whether this situation will persist is unclear in view of events over which the industry has little or no direct controls.

Of particular concern is the growing interest of resource adjacent nations to develop their own tuna fisheries, or otherwise benefit from readily accessible tuna resources. Whether the western Pacific will continue to account for the largest share of the U.S. tuna catch will depend on access and fishery development agreements that can be negotiated with the numerous island governments that exist in this region. In this regard, future stability in the exploitation of western Pacific tuna resources would seem contingent on the creation of a cohesive institutional arrangement that recognizes resource limitations as well as the particular interests of all parties involved. In addition, adequate industry infrastructure must be in place to support future growth. Similar concerns can be expressed over potential expansion of the U.S. tropical tuna fleet into the Atlantic and Indian Oceans. On the other hand, the eastern Pacific could regain its former harvesting stature once the effects of El Niño have completely abated and the pending international access licensing arrangement, the "Eastern Pacific Ocean Tuna Fishing Agreement," in this area is fully endorsed.

The U.S. industry has also expressed considerable alarm over the recent influx of canned tuna imports. Production of canned tuna outside the United States has grown steadily over the last decade. Most of this increase has been targeted for export to the United States, the major market for canned tuna, where the market share of imports has more than doubled in recent years from 6 percent in 1977 to 14 percent in 1982. In terms of total volume, U.S. imports of canned tuna increased 136 percent between 1978 and 1983 (72 percent from 1981 to 1983), an annual average rate of 19 percent. On the other hand, during this same period, imports of raw tuna decreased almost 43 percent, a significant shift in U.S. tuna imports from raw to finished product. Foreign producers thus gain the value added through processing. This implies a real cost-revenue squeeze for U.S. processors as they compete with foreign processors for inputs of raw tuna, driving up production costs and as they compete with foreign processors to maintain their share of domestic retail sales, putting downward pressure on prices they receive. Domestic wholesale prices fell to low levels in 1983, and discounts of up to $9.00 per case were also being offered; nonetheless, import prices were still from $3.00 to $5.00 per case below domestic prices. Lower production costs and a strong U.S. dollar abroad have made foreign produced canned tuna very attractive to U.S. importers since early 1982. Furthermore, since the ad valorem duties on canned tuna imports are determined by their price, the lower the price of imported canned tuna, the lower the customs duty. The current high value of the U.S. dollar acts to further reduce the effective tariff on imported canned tuna. Even if the dollar weakens against foreign currencies in the near term, U.S. producers will continue to face stiff competition from foreign processors.

A significant event affecting the tuna industry in 1983 was the exclusion of canned tuna not in oil packed in American Samoa from being counted against the quota on imports of canned tuna not in oil. It is estimated that one-third of the annual quota in recent years had been filled by canned tuna processed in American Samoa. In effect, the American Samoa exclusion allows foreign countries to export that much more canned tuna not in oil under the lower tariff duty rate. To a great extent this accounts for the large increase in foreign produced canned imports in 1983.

The U.S. tuna industry has brought attention to the import situation by seeking revisions to the tariff structure for tuna imports not in oil. It also successfully petitioned for a countervailing duty investigation on imported canned tuna from the Philippines. The investigation resulted in a countervailing duty of 0.72 percent being levied against Philippine exporters to offset production subsidies they received. This is the only case where the U.S. industry has obtained import relief, and it proved to be very minor, but as foreign competition grows more intense, it is likely that the U.S. industry will pursue other means available to protect itself as it adjusts to a new international order in tuna harvesting and processing.

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PELAGIC FISHERIES RESOURCES OF THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

Included in this paper are reviews of data collected by the Hawaii Division of Aquatic Resources on the fish catch in the Northwestern Hawaiian Islands (NWHI) by longlining and trolling in recent years, the relatively new fishery for albacore, Thunnus alalunga, in the vicinity of the NWHI that is being carried out by U.S. West Coast albacore trollers, and some of the longline, live-bait, and gill-net fisheries that are being carried out by Japanese and Taiwan vessels in the North Pacific Ocean.

gill net
longline
troll
live bait
pelagic fisheries
Northwestern Hawaiian Islands

INTRODUCTION

The purpose of this report is to review some of the pelagic fisheries within the 200-mile U.S. fishery conservation zone around the Northwestern Hawaiian Islands.

DOMESTIC CATCHES IN THE NORTHWESTERN HAWAIIAN ISLANDS

The commercial fish landing reports of the Division of Aquatic Resources (DAR) of the Hawaii Department of Land and Natural Resources from 1971 through 1980 show that fish harvested in the NWHI ranged from 23 to 108 metric tons (MT) (Table 1). Besides the total landings, shown in parentheses are the catches of pelagic species. The amount of pelagic species caught fluctuated from 1.7 to 9.4 MT and represented 2 to 26 percent of the fish caught in the NWHI, with an average of 11 percent. Table 2 shows the catch by species for the same years. The catches of 245 to 6,700 kg of yellowfin tuna, Thunnus albacares, and 760 to

3,730 kg of wahoo, Acanthocybium solandri, were the largest contributors to the pelagic fish landings. Kawakawa, Euthynnus affinis, made a noticeable contribution of 1,200 kg in 1975, as well as skipjack tuna, Katsuwonus pelamis, with a catch of 3,260 kg in 1979. These data show that the amount of pelagic species caught in the NWHI contributed less than 1 percent of the state's annual fish landings. This indicates that the pelagic fish resources are either very scarce in the NWHI or that pelagic species are not being fished very hard. It seems that the latter is true -- that pelagic resources in the NWHI are not being utilized to any significant extent by Hawaiian fishermen.

TABLE 1. COMMERCIAL LANDINGS OF FISH CAUGHT IN THE NORTHWESTERN HAWAIIAN ISLANDS, 1971-80

Year	Metric Tons Sold	Value
1971	36.5 (2.4)	$ 52,848
1972	23.4 (4.0)	46,282
1973	30.8 (2.8)	65,979
1974	25.2 (2.7)	53,277
1975	36.4 (9.4)	70,439
1976	35.0 (8.1)	89,272
1977	64.0 (2.2)	279,366
1978	94.9 (1.7)	360,742
1979	66.4 (8.8)	260,655
1980	107.5 (2.5)	623,479

Source: Data from Hawaii Division of Aquatic Resources

Note: Contribution to the landings by pelagic species given in parentheses

PELAGIC FISH OBSERVATIONS IN THE NORTHWESTERN HAWAIIAN ISLANDS

The data collected from the bird flock and fish school observations made on the cruises of the Townsend Cromwell in the NWHI from 1976 to 1982 were analyzed since bird flocks are known to be associated with fish schools. Their abundance would theoretically reflect pelagic fish school abundance. The recorded observations were summarized by three subareas (Figure 1). Subarea I includes Nihoa, Necker Island, and French Frigate Shoals. Subarea II includes Gardner Pinnacles, Laysan Island, and Lisianski Island. Subarea III includes Pearl and Hermes Atoll, Midway Islands, and Kure Atoll.

TABLE 2. COMMERCIAL LANDINGS (KILOGRAMS) OF PELAGIC SPEICES FROM THE NORTHWESTERN HAWAIIAN ISLANDS, 1971-80

Species	Year									
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
Yellowfin tuna	1,043	1,069	374	1,152	6,700	4,266	1,106	660	1,699	245
Kawakawa	40	80	146	373	1,204	109	197	100	496	301
Mahimahi	240	161	334	235	151	30	9	54	14	160
Wahoo	975	2,717	1,909	910	747	3,727	758	907	3,268	1,688
Rainbow runner	36	—	—	—	11	—	—	7	36	48
Skipjack tuna	38	—	—	—	632	—	97	—	3,260	—
Broadbill	—	—	—	—	—	—	—	—	64	—
Blue marlin	—	—	—	—	—	—	—	—	—	79
Shortbill spearfish	—	—	—	—	—	—	—	—	—	8
TOTAL	2,372	4,027	2,763	2,670	9,445	8,132	2,167	1,728	8,837	2,529

Source: Data from Hawaii Division of Aquatic Resources

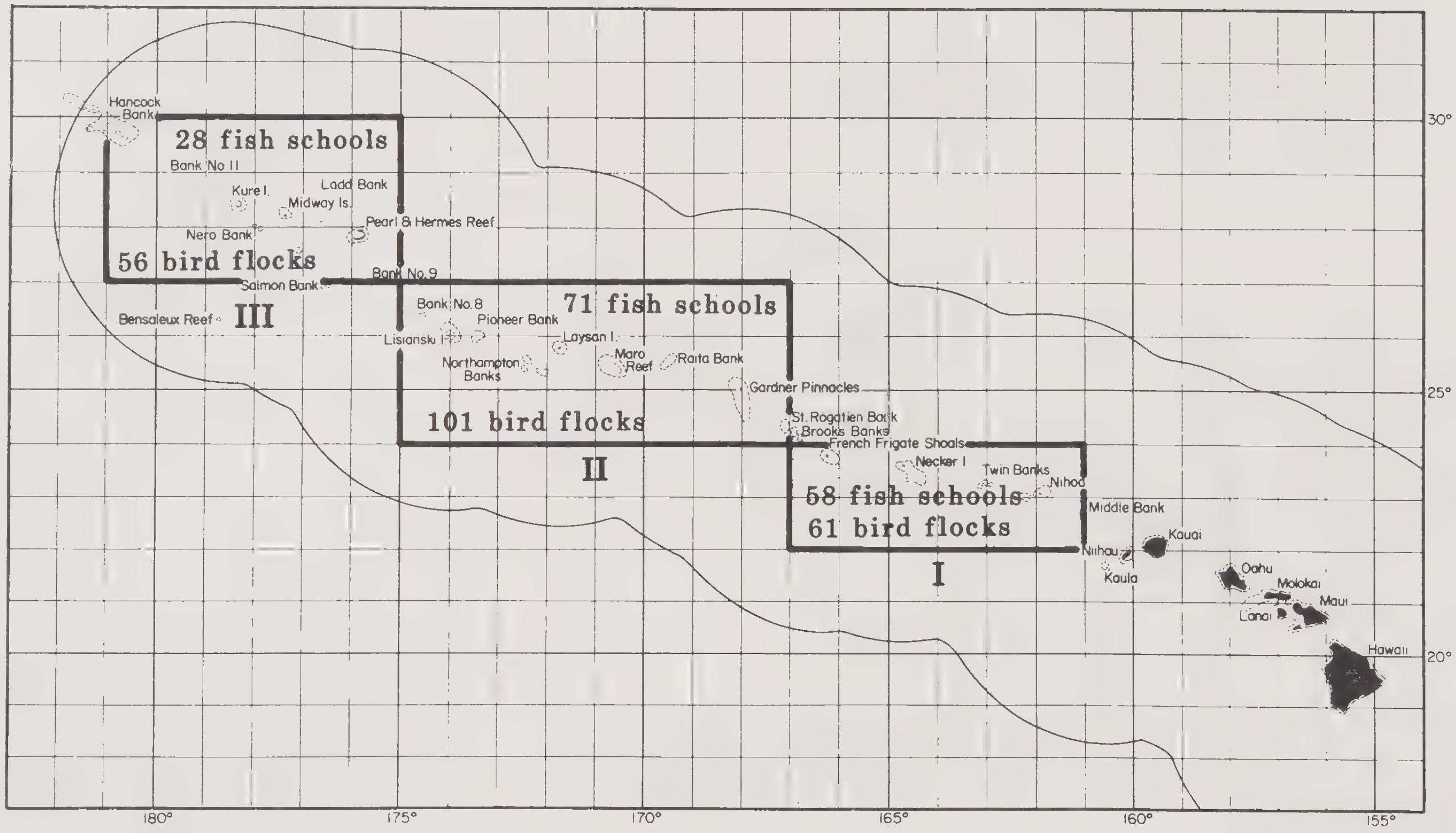
Hancock Bank
28 fish schools
Bank No 11
Kure I.
Ladd Bank
Midway Is.
Pearl & Hermes Reef
Nero Bank
56 bird flocks
Salmon Bank
Bank No.9
Bensaleux Reef
III
Bank No.8
Pioneer Bank
71 fish schools
Lisianski I.
Laysan I.
Maro Reef
Raita Bank
Northampton Banks
Gardner Pinnacles
101 bird flocks
St. Rogatien Bank
Brooks Banks
French Frigate Shoals
II
Necker I.
Twin Banks
Nihoa
58 fish schools
61 bird flocks
Middle Bank
Kauai
Niihau
Kaula
I
Oahu
Molokai
Maui
Lanai
Hawaii
30°
25°
20°
180°
175°
170°
165°
160°
155°

Figure 1. The number of fish schools and bird flocks observed on cruises of the _Townsend Cromwell_ in three subareas in the Northwestern Hawaiian Islands, 1977-82

Bird Flocks

The total numbers of bird flocks and fish schools sighted were 61 in subarea I, 101 in subarea II, and 56 in subarea III. Well over 50 percent of the bird flocks seen in each area were made up of flocks estimated to have 26 to 100 seabirds. It was noted that the larger flocks of over 100 birds were more numerous in subareas II and III where they accounted for 29 to 34 percent of the flocks recorded.

Fish Schools

Of the 58 fish schools recorded for subarea I, 12 were porpoises (Delphinidae), 9 were skipjack tuna, 5 were kawakawa, 3 were yellowfin tuna, and 4 were mixed tuna schools. Of the 71 fish schools observed in subarea II, 16 were porpoises, 13 were yellowfin tuna, 6 were kawakawa, 4 were skipjack tuna, and 3 were flyingfish (Exocoetidae). Of the 28 schools sighted in subarea III, 4 were porpoises, 4 were yellowfin tuna, 3 were kawakawa, and 2 were flyingfish. Thirty-eight percent of the fish schools sighted could not be identified.

Trolling

Besides observing bird flocks and fish schools while on the cruises of the *Cromwell*, trolling was conducted whenever possible. Trolling catches were also summarized by the same three subareas. The trolling records show that 284 fishes were caught in subarea I, 332 fishes in subarea II, and 123 fishes in subarea III. Of the 284 fishes caught in subarea I, 190 (67 percent) were kawakawa, 44 (16 percent) were yellowfin tuna, and 19 (7 percent) were wahoo. In subarea II, of the 332 fishes caught, 181 (54 percent) were kawakawa, 55 (17 percent) were yellowfin tuna, and 46 (14 percent) were wahoo. Of the 123 fishes caught in subarea III, 72 (58 percent) were yellowfin tuna, 22 (18 percent) were skipjack tuna, and 20 (16 percent) were kawakawa. The average size of the species caught were as follows: skipjack tuna, 2.8 kg; yellowfin tuna, 8.6 kg; wahoo, 13.9 kg; kawakawa, 2.8 kg,; and mahimahi, *Coryphaena hippurus*, 6.2 kg.

FOREIGN FISHERIES IN THE NORTHWESTERN HAWAIIAN ISLANDS

Longliners

Yong and Wetherall (1980) made estimates of catches by Japanese longliners within the 200-mile U.S. fishery conservation zone in the NWHI for the years 1971 through 1977 (Table 3). The catches of albacore, *T. alalunga*, ranged from 170 to 910 MT during these years. Yellowfin tuna catches ranged from 120 to 470 MT and bigeye tuna, *T. obesus*, catches ranged from 100 to 1,300 MT. Only negligible catches of skipjack tuna and bluefin tuna, *T. thynnus*, were made. The annual tuna catches ranged from 500 MT in 1974 to 2,400 MT in 1976.

TABLE 3. ESTIMATED CATCH (METRIC TONS) BY JAPANESE LONGLINERS IN THE NORTHWESTERN HAWAIIAN ISLANDS, 1971-77

Species	Year						
	1971	1972	1973	1974	1975	1976	1977
Albacore	398	478	348	281	170	912	446
Yellowfin tuna	467	268	133	119	171	330	304
Bigeye tuna	821	1,284	496	95	512	1,155	1,510
Skipjack tuna	2	2	2	2	2	1	1
Bluefin tuna	1	2	1	1	1	1	1
Total tunas	1,689	2,034	980	498	856	2,399	2,262
Blue marlin	81	62	18	24	14	22	26
Striped marlin	261	173	78	20	70	136	113
Broadbill	63	192	89	45	27	220	57
Black marlin	4	2	1	1	1	1	2
Spearfish and sailfish	8	8	10	7	7	8	5
Total billfishes	417	437	196	97	119	387	203
Grand total	2,106	2,463	1,176	595	975	2,786	2,465

Source: Data from Yong and Wetherall, 1980

Among the billfishes, catches ranged from 27 to 220 MT for swordfish, *Xiphias gladius*, 20 to 261 MT for striped marlin, *Tetrapturus audax*, and 14 to 81 MT for blue marlin, *Makaira nigricans*. Only small amounts of black marlin, *M. indica*, shortbill spearfish, *T. angustirostris*, and sailfish, *Istiophorus platypterus*, were caught. The annual billfish catches ranged from 97 to 437 MT. The annual catches of tunas and billfishes by Japanese longliners during these years ranged between 600 and 2,800 MT and averaged 1,800 MT.

The number of days fished in the NWHI by the Japanese longliners from 1971 to 1975 ranged from a low of 444 to a high of 1,747. Based on 2,000 hooks fished per day, Yong and Wetherall calculated catch per unit of effort for these vessels to be 14 to 19 tunas per 1,000 hooks fished (28 to 38 per day). The catch per unit of effort for billfishes ranged from two to three per 1,000 hooks fished (four to six per day).

Bait Boats

Yong and Wetherall also made estimates of catches by Japanese bait boats within the 200-mile U.S. fishery conservation zone in the NWHI from 1972 through 1977 (Table 4). The annual skipjack tuna catches ranged from 823 to 4,375 MT. Annual catches of some of the other tunas ranged from 20 to 337 MT for yellowfin tuna, and 71 to 734 MT for bigeye tuna. Albacore and bluefin tuna were, at times, caught only in small quantities. The annual catches made by these bait boats ranged from 964 to 5,619 MT.

It was reported that bait boats fishing within 200 miles of the NWHI made catches of 20 to 90 MT per day of mixed small skipjack, yellowfin, and bigeye tunas when fishing was good in May of 1977 and 2 to 4 MT per day when fishing was poor in June and July of 1977 (Tanaka, 1978). It was also reported that four to five bait boats fishing within 200 miles of the NWHI in May of 1979 made catches of 7 to 38 MT of mixed skipjack, yellowfin, and bigeye tunas per day, averaging 8 to 10 MT per day (Tanaka, 1980).

TABLE 4. ESTIMATED CATCH (METRIC TONS) BY JAPANESE BAIT BOATS IN THE NORTHWESTERN HAWAIIAN ISLANDS, 1972-77

Species	Year					
	1972	1973	1974	1975	1976	1977
Albacore	26	0	0	89	0	49
Yellowfin tuna	19	20	50	167	124	337
Bigeye tuna	105	109	147	71	92	734
Skipjack tuna	1,282	823	1,971	1,906	4,294	4,375
Bluefin tuna	26	0	1	25	0	0
Total tunas	1,458	952	2,168	2,258	4,510	5,495
Others	37	12	25	94	37	124
Grand total	1,495	964	2,193	2,352	4,547	5,619

Source: Data from Yong and Wetherall, 1980

NORTH PACIFIC ALBACORE FISHERIES

The North Pacific albacore fisheries extends throughout the North Pacific. The albacore landings made by Japanese longline and surface (pole-and-line) fisheries, the North American fishery, and the total landings from 1961 through 1981 as presented by Majors et al. (1982) are shown in Figure 2. The catch figures are complete only up to 1979 for all fisheries.

The catches made by the Japanese longline fishery have not fluctuated very widely with a low of 10,000 MT in 1975 and a high of 29,000 MT in 1967. The Japanese longliners fish in the North Pacific subtropical zone during winter. It has been estimated that 40 percent of the catch (by number) is albacore (Laurs et al., 1981). The area where they operate centers on lat. 32°N and extends from 800 nmi off the coast of California westward across the Pacific. The total albacore landings fluctuated between 47,000 MT in 1962 and 124,000 MT in 1976 in the North Pacific and reflect the fluctuations of the Japanese surface catches which ranged from a low of 9,000 MT in 1962 to a high of 85,000 MT in 1976. The catches made by U.S. jig boats have fluctuated between 10,000 MT in 1977 and 25,000 MT in 1963.

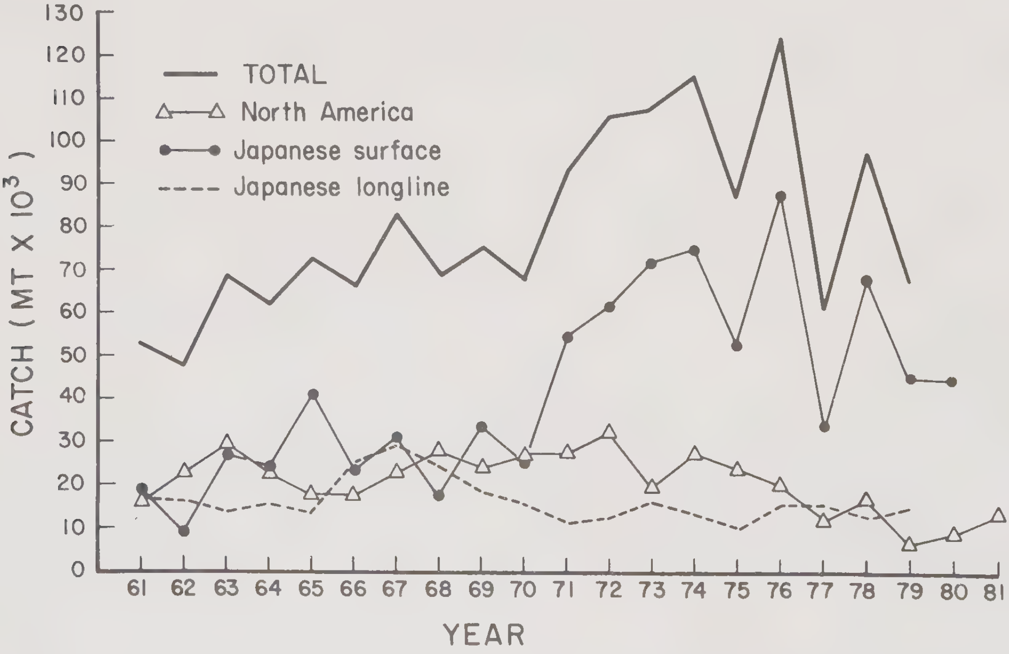

Figure 2. The total albacore catch in the North American and the Japanese longline and surface fisheries, 1961-81 (Majors et al., 1982)

In recent years, there has been increased interest by U.S. West Coast trollers to fish in waters northwest of Midway. The Pacific Tuna Development Foundation sponsored exploratory fishing surveys by West Coast trolling boats in areas northwest of Midway from 1975 to 1978. The surveys showed that trolling for albacore in this area was practical for U.S. fishermen. In 1979, the state of Hawaii and a private seafood processor obtained a 1-year use permit from the Navy and organized a mother ship operation at Midway supporting 20 albacore trollers that fished to the northwest of the island. This undertaking resulted in a catch of 2,000 tons of albacore which was valued at more than $3 million.

The state attempted to organize support operations for the albacore trollers in 1980, 1981, and 1982 but were not able to do so. The albacore trollers, however, fished the area northwest of Midway in increased numbers and unloaded most of their catch in Dutch Harbor, Alaska.

In 1981, an estimated 47 albacore trolling boats fished in the area and landed an estimated 754 tons of mostly albacore in Honolulu (B.M. Ito, 1983: personal communication). This catch was made in 38 trips which gave a catch rate of 20 tons per trip. In 1982, about 54 boats fished in the area and landed their catch in Honolulu (B.M. Ito, 1983: personal communication). The catch from 73 trips amounted to 1,858 tons which gave a catch rate of 25 tons per trip.

In 1982, the Hawaii Legislature appropriated funds to do a feasibility study for establishing a Midway fishery support base. DAR was given the responsibility for implementing the project.

At the present time, about a dozen albacore trolling boats have left Honolulu and are headed for the fishing grounds to the northwest of Midway.

OTHER PELAGIC FISHERIES

One of the fisheries that is distant from the NWHI is a gill-net fishery for squid centered on the Emperor Seamount fishing grounds. The primary species is *Ommastrephes bartramii*. It was reported that 79 Taiwan gill-net vessels, 200 Japanese squid jigging vessels, and about 200 Japanese squid gill-netting vessels were fishing in August of 1981 (Suisan Sekai, 1981). The Taiwan vessels reportedly made good catches of 3 to 6 tons of squid per day.

The Japanese made a gill-netting survey from April 1979 to January 1980 in subarctic waters in the North Pacific for pomfret, *Brama japonica*, and salmon shark, *Lamna ditropis* (Japan Marine Fishery Resource Research Center, 1980-81). Catches on five cruises within that timespan included the following: pomfret, 247 MT; blue shark, *Prionace glauca*, 180 MT; albacore, 180 MT; and salmon shark, 86 MT. Total catch amounted to 806 MT.

Closer to Hawaii, a Japanese gill netter operating for 29 days within 200 miles of the NWHI during February and March caught 57 striped marlin, 12 swordfish, 872 albacore, 2,191 skipjack tuna, 331 mahimahi, 659 pomfret, 152 amberjack, *Seriola* sp., 682 squids, 32 sharks, and 23 bigeye tuna (NMFS unpublished data).

A Japanese gill-net fishery for North Pacific albacore, which made nominal catches of between 1,000 and 4,000 MT per year since its inception in the early 1970s up until 1980, caught an estimated 15,000 to 20,000 MT in 1981 (Bartoo and Kume, 1982).

CONCLUSIONS

This review shows that pelagic fisheries resources in the NWHI area have been utilized by Japanese bait boats and longliners. It also shows that U.S. West Coast trollers are increasing effort to harvest albacore and possibly other species in the area.

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THE STRUCTURE OF REEF FISH COMMUNITIES IN THE HAWAIIAN ARCHIPELAGO

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ABSTRACT

The great variety of reef habitats in the Hawaiian Archipelago has a profound influence on how the species of reef fishes are distributed. For some species, however, the pattern has been strongly modified by fishing pressures. The fauna is basically derived from the tropical western Pacific, a relationship that is generally most evident in communities at the southeastern end of the archipelago, but is also particularly evident at French Frigate Shoals which is located at the center of the archipelago. Although communities at the northwestern end of the archipelago similarly show close ties to the tropical Pacific, they also include species from more temperate regions of the western Pacific. These more temperate derivatives decrease in numbers and/or occur in deeper water southeastward. Conversely, some deep-water tropical forms that exist only on deeper reefs in the southeast occur on shallow reefs in the northwest. The predominant members of the northwestern communities, as a group, are better tuned to the overall Hawaiian environment than are the predominant members of the southeastern communities. They show this by being more evenly distributed over the archipelago and by including proportionally more endemics. The southeastward distributions of species in the northwestern communities are limited by both environmental and fishing pressures, but the northwestward distributions of species in the southeastern communities are limited only by environmental factors.

fishes
Hawaii
fish communities
zoogeography

INTRODUCTION

The distribution of reef fish species in Hawaii is strongly influenced by the great diversity of reef habitats over the archipelago. Because each species' occurrence is defined by a combination of characteristics adapted to specific environmental conditions, its greatest numbers should occur where these conditions are best approximated. But patterns of occurrence no doubt have been distorted by fishing pressures, which have been species and area specific. These opinions remain largely conjectural because the actual patterns of distribution for the various species remain poorly known. This study was undertaken to improve and expand our knowledge of these relationships for the purpose of developing more effective management guidelines.

REEF HABITATS

Reef habitats in the Hawaiian Archipelago range from those that fringe the massive volcanic island of Hawaii, to those located more than 1,500 km northwestward that are the major structure of Kure Atoll. Each of the major high islands offers many distinct habitats, but it is a mix that tends to recur because these islands have similar topographies. Being in essence one or more large volcanic peaks that block the prevailing wind and seas, the high islands support distinctive windward and leeward reefs. Furthermore, so abrupt is their rise from great ocean depths that room for nearshore reefs is limited.

In contrast, highly dissimilar underwater settings exist from one end of the Northwestern Hawaiian Islands to the other. In part, this is because they cover almost three times the distance and more than twice the latitude of the high islands. Probably more important, however, is the fact that their topographies are more varied. Nihoa and Necker are most like the high islands, being small volcanic peaks that rise abruptly from the sea. But they offer no appreciable lee, and both rest on broad submerged platforms that provide more suitable depths for shallow habitats than do the comparatively narrow shelves that surround the high islands. Northwestward from Necker, conditions progressively become even more different. At French Frigate Shoals exposed volcanic rock is limited to La Perouse Pinnacle, a basaltic structure that juts from amid expansive shallows and low sandy islets. This and Gardner Pinnacles -- two precipitous volcanic rocks surrounded by a broad submerged platform -- are the last bits of exposed basalt to the northwest. Farther on, Maro Reef is the almost totally submerged crest of an oval-shaped seamount, whereas Laysan and Lisianski are low sandy islands surrounded by wide shallows. Finally, Pearl and Hermes, Midway, and Kure are coral atolls, even though they lie at high latitudes.

METHODS

Between 1977 and 1982, reef fish communities between shore and depths of 20 to 35 m were assessed throughout the archipelago (Table 1). Because the various stations were sampled at different times during different seasons, often 1 or more years apart, it was important to know how much the species composition of the fish communities could be expected to vary over time. For this reason, assessments were repeated over 2 or more years in selected locations at each end of the archipelago. A site off the island of Hawaii was sampled throughout the 5 years of the study, including all seasons, and a site off Midway was sampled over 2 years, including two seasons. Repeated counts and observations also were made at several other sites during the study, but because the results relevant to this question were the same as for the stations off Hawaii and Midway, they are not presented in this paper. In general, however, the limited number of opportunities available to sample this vast area, with so many habitats, precluded replicate assessments at specific stations.

TABLE 1. ASSESSMENT OF REEF FISH COMMUNITIES AT VARIOUS STATIONS IN THE HAWAIIAN ARCHIPELAGO, JULY 1977 TO OCTOBER 1982

Station	No. of Habitats	No. of Transects	Transect Depths (m)
Hawaii	6	54	2-12
Oahu	6	17	5-12
Niihau	2	4	7-10
Nihoa	2	5	8-10
Necker Island	2	3	10-15
French Frigate Shoals	8	11	9-15
Gardner Pinnacles	3	3	10-12
Maro Reef	3	4	2-12
Laysan Island	4	4	3-16
Lisianski Island[1]	5	5	7-10
Pearl and Hermes Atoll	2	2	7-12
Midway Islands	8	16	2-12
Kure Atoll	8	14	2-12

[1] Including Neva Shoal

A standard procedure was used at all the islands in order to obtain comparable data. First, a general reconnaissance was made to obtain provide familiarity with the area and fauna, identify representative habitats, and provide a list of the species present. Then in each representative habitat the community was characterized upon conducting two consecutive visual counts of the fishes in 4 m x 25 m transects. The intent was to determine which species frequented the sampled habitat and not to measure the existing biomass. Forty minutes were spent tabulating species on each transect. The final tally included many more individuals than were present in the sampled area at any one moment. Other details of the procedures used in making the counts are reported in Hobson (1980).

Counts were limited to individuals that appeared and behaved as adults because the occurrences of many juveniles varied greatly with season and from year to year for reasons unrelated to conditions on the reef. Inclusion of juveniles would have, in fact, obscured rather than clarified the zoogeographic questions considered in this paper.

Owing to limitations in the visual sampling method, highly cryptic forms such as muraenid eels are greatly underrepresented. Also, in some habitats the same is true of certain nocturnal species, such as holocentrids, that spend the daytime under cover. However, because this bias was constant throughout the study, the counts should illustrate any major differences in numbers of individuals of these species between sites.

Non-reef species that occurred near the reefs were excluded from the counts. These include certain small forms, such as atherinids and engraulids, that occurred just under the water's surface and also small benthic forms, such as gobiids, that often were abundant on the sand adjacent to the reef.

Following each count the surrounding area was inspected for other species, noting their relative numbers and any indications that the transect counts might have produced a misleading assessment of the community. These supplemental observations contributed to the interpretations drawn from the transect data and are especially important as added support when a species was noted as absent. The comparisons are limited to observations made during this study in order to reduce the bias that otherwise would stem from including the many observations made during other studies in previous years in the high islands, especially around Oahu and Hawaii.

RESULTS

Temporal Patterns

The major components of the reef fish communities remained relatively unchanged at the sites on Hawaii and Midway (Table 2). The 10 most numerous species at the time of the first counts at each site continued (with a few exceptions among the lower-ranked forms) to maintain similar proportions in the same communities in later years.

TABLE 2. TEMPORAL VARIATIONS IN FISH COMMUNITIES ON TWO HAWAIIAN REEFS

LEEWARD HAWAII	Jul 1977	Oct 1978	Sep 1979	Apr 1980	Oct 1982
Number of Transects	4	4	4	2	2
$\bar{x}$ Species	34	33	35	31	34
$\bar{x}$ Individuals	185	159	191	158	188
1977 Species Ranking	Relative Abundance Index[1]				
Chromis agilis	19.1	18.0	18.5	18.0	13.9
Ctenochaetus strigosus	12.7	15.8	15.4	13.2	17.6
Zebrasoma flavescens	12.1	16.6	13.8	17.2	23.2
Chaetodon multicinctus	8.4	10.1	8.3	9.4	6.4
Chromis vanderbilti	6.3	0.9	4.7	4.1	0
Thalassoma duperrey	6.1	4.4	3.4	4.1	1.9
Acanthurus nigrofuscus	4.4	1.7	1.0	0	0.8
Plectroglyphidodon johnstonianus	3.3	3.0	1.8	2.5	2.5
Centropyge potteri	3.1	3.3	3.8	3.5	3.5
Chromis hanui	2.4	2.8	1.8	1.9	0.8

WINDWARD MIDWAY	Aug 1977	Sep 1979
Number of Transects	2	2
$\bar{x}$ Species	33	35
$\bar{x}$ Individuals	316	223
1977 Species Ranking	Relative Abundance Index[1]	
Acanthurus triostegus	16.3	11.7
Chromis ovalis	14.2	13.9
Acanthurus leucopareius	12.3	12.8
Myripristis amaenus	7.0	6.1
Stegastes fasciolatus	6.3	8.5
Kyphosus bigibbus	5.4	4.9
Thalassoma duperrey	4.9	8.5
Acanthurus nigroris	4.7	0.4
Abudefduf abdominalis	2.7	7.6
Thalassoma ballieui	1.9	2.9

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[1] Relative Abundance Index is the percentage of all individuals counted that were of this species.

Spatial Patterns

The species constituting the reef fish communities varied greatly from one reef habitat to another, but there were broad similarities in certain basic features. Although there were 30 to 40 species in most of the communities, just three or four of them included over 50 percent of the individuals present. Typically, one species included 15 to 20 percent of all individuals, whereas the other two or three species included 10 to 15 percent each. These major species, which differed from one habitat to another, presumably are those best attuned to the prevailing environment and thus probably can be considered characteristic of that particular habitat. It is instructive, therefore, to consider the distribution throughout the archipelago of species that were major forms in any one of the many distinctive communities examined (Table 3). Species included in this list are those that comprised at least 10 percent of the individuals counted in two or more transects in any one habitat.

These major species generally were most prominent at one or the other end of the archipelago. Significantly, those that predominated in the northwestern communities tended to be more evenly distributed over the archipelago than those that predominated in the southeastern communities. Thus, although the northern dominants -- *Myripristis amaenus*, *Kyphosus bigibbus*, *Chromis ovalis*, *Stegastes fasciolatus*, *Thalassoma duperrey*, *T. ballieui*, *Acanthurus leucopareius*, *A. nigroris*, and *A. triostegus* -- declined somewhat in numbers southeastward, the trend was uneven, and all were relatively numerous, if not dominant, throughout the archipelago. In comparison, the southern dominants -- *Chaetodon multicinctus*, *Chromis agilis*, *C. vanderbilti*, *Acanthurus nigrofuscus*, *Ctenochaetus strigosus*, and *Zebrasoma flavescens* -- lost dominance at some point northwestward and hence were few or absent at Midway and Kure.

The numbers of some prominent members of the northwestern communities declined sharply southeastward until at some point they were absent from the shallow reefs. Consider those species that occurred in two or more transects in any one habitat at Kure or Midway, but which were not seen off the island of Hawaii (Table 4). Three -- *Pristilepis oligolepis*, *Epinephelus quernus* (Figure 1), and *Oplegnathus fasciatus* -- were seen nowhere else, while two others -- *Oplegnathus punctuatus* and *Carangoides othogrammus* -- occurred southward only in sharply reduced numbers -- the former to Maro Reef, the latter to Nihoa. Two -- *Cheilodactylus vittatus* and *Epibulus insidiator* -- were relatively numerous at French Frigate Shoals, but were not seen farther south, and the other two -- *Carcharhinus amblyrhynchos*, and *Caranx ignobilis* (Figure 2) -- were numerous all the way to Nihoa, but were not seen in the major high islands during this study period. Two other species seen repeatedly on reefs as shallow as 20 m at Midway and Kure, but not in the transects,

TABLE 3. DISTRIBUTION OF MAJOR REEF FISHES THROUGHOUT THE HAWAIIAN ARCHIPELAGO

Species	Location[1]													
	Hl	Hw	Ol	Ow	NI	NE	FFS	GP	MR	LA	LI	PH	MKl	MKo
Myripristis amaenus	<0.1	●[2]	0[2]	0	●	0	0.1	0.2	0.1	<0.1	0	0.3	0	2.3
Kyphosus bigibbus	<0.1	●	●	0.1	4.4	0.2	0.6	6.0	0.8	4.6	0.2	3.1	2.2	5.9
Chaetodon multicinctus	4.7	3.2	5.0	0.2	0.8	0.6	0.8	0	0	1.3	0	0.1	0	<0.1
Stegastes fasciolatus	1.2	5.9	4.6	6.5	3.1	4.5	2.2	9.4	13.8	4.2	5.0	1.5	18.0	7.2
Plectroglyphidodon imparipennis	0.8	<0.1	●	1.7	1.7	0.7	0.4	1.0	0	0	0	0	0	0
Dascyllus albisella	●	0	●	●	0	●	2.8	0	<0.1	0	0.4	●	0.3	0
Chromis agilis	3.8	0.2	0.1	0	0	0	<0.1	0	0	0	0	0	0	0
C. ovalis	●	0.2	7.1	4.2	2.4	7.5	6.8	3.4	16.2	26.2	●	39.7	0.1	18.3
C. vanderbilti	5.7	4.0	<0.1	6.8	23.6	6.6	3.7	22.3	0	0.6	0	2.4	0	0.1
Thalassoma ballieui	<0.1	<0.1	0.4	0.2	<0.1	1.6	1.5	2.0	2.1	2.5	2.4	1.0	6.3	2.3
T. duperrey	4.8	4.0	6.0	10.6	4.8	13.9	7.0	6.2	8.8	4.8	9.9	1.2	18.9	10.4
Acanthurus leucopareius	0.3	<0.1	0	0.6	0.6	0.3	<0.1	●	●	0.4	●	0.1	0	5.4
A. nigrofuscus	8.6	9.3	11.2	9.8	5.6	0.7	1.4[3]	0.7	●	<0.1	0	0	0	0
A. nigroris	0.4	0.8	0.4	0	2.3	2.0	1.8	5.5	6.0	4.3	9.1	0.9	0.7	8.6
A. triostegus	0.2	0.1	0.6	0.5	0.1	2.0	0.5	4.7	7.4	<0.1	4.9	0.5	2.0	4.7
Ctenochaetus strigosus	13.1	13.5	9.3	1.7	3.4	0	7.0	0.2	2.2	1.4	7.5	1.2	1.4	0.4
Zebrasoma flavescens	16.6	0.7	1.5	0	<0.1	0	0.8	0	●	<0.1	<0.1	0.4	●	0
Melichthys niger	0.1	0.1	<0.1	0	0.2	0.3	8.1	3.0	<0.1	3.0	●	5.8	0	0.9
Pervagor spilosoma	<0.1	0	1.3	1.0	0	0.2	0.4	<0.1	0	1.1	8.8	0.1	<0.1	0

Note: Values given are occurrence indices, which are the product of the mean relative abundance index and frequency of occurrence for all transects at each location.

[1] Hl = Hawaii: leeward; Hw = Hawaii: windward; Ol = Oahu: leeward; Ow = Oahu: windward; NI = Nihoa; NE = Necker Island; FFS = French Frigate Shoals; GP = Gardner Pinnacles; MR = Maro Reef; LA = Laysan Island; LI = Lisianski Island; PH = Pearl and Hermes Atoll; MKl = Midway Islands - Kure Atoll: lagoons; MKo = Midway Islands - Kure Atoll: outside barrier reefs

[2] ● = seen but not on transect; 0 = not seen

[3] Virtually all *A. nigrofuscus* at La Perouse Pinnacle; occurrence index there: 8.0 (4 transects)

TABLE 4. OCCURRENCES OF SPECIES COUNTED IN TWO OR MORE TRANSECTS IN ANY ONE HABITAT MOVING SOUTHEASTWARD IN THE HAWAIIAN ARCHIPELAGO

Species	Location[1]												
	KA	MI	PH	LI	LA	MR	GP	FFS	NE	NI	NU	OA	HI
Carcharhinus amblyrhynchos	*	*	*	*	●	●	●	*	*	x			
Pristilepis oligolepis	*	●											
Epinephelus quernus	*	*											
Oplegnathus fasciatus	●	*											
O. punctatus	x	*			●	●							
Cheilodactylus vittatus	*	*	●			●	x	x					
Caranx ignobilis	*	*	*	*	x	*	*	*	●	●			
Pseudocarnx dentex	●	*											
Carangoides othogrammus	*							*		●			
Epibulus insidiator	*	*	*	x		x		*					

Note: * = occurring in two or more transects; x = occurring in one transect; ● = seen. None were seen off Niihau, Oahu, and Hawaii.

[1] KA = Kure Atoll; MI = Midway Islands; PH = Pearl and Hermes Atoll; LI = Lisianski Island; LA = Laysan Island; MR = Maro Reef; GP = Gardner Pinnacles; FFS = French Frigate Shoals; NE = Necker Island; NI = Nihoa; NU = Niihau; OA = Oahu; HI = Hawaii

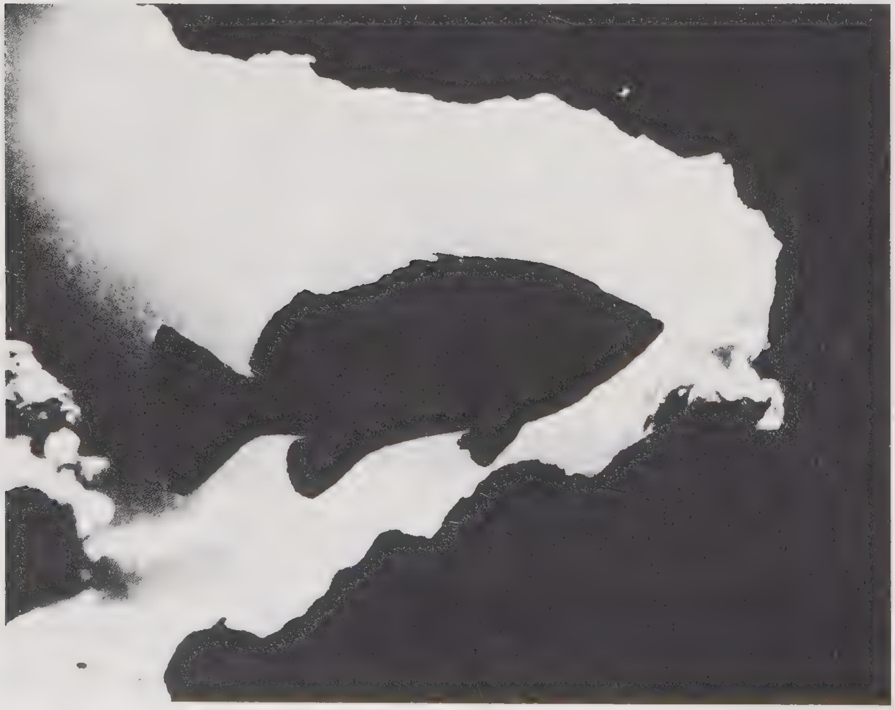

Figure 1. *Epinephelus quernus* on a reef 10 m deep at Midway

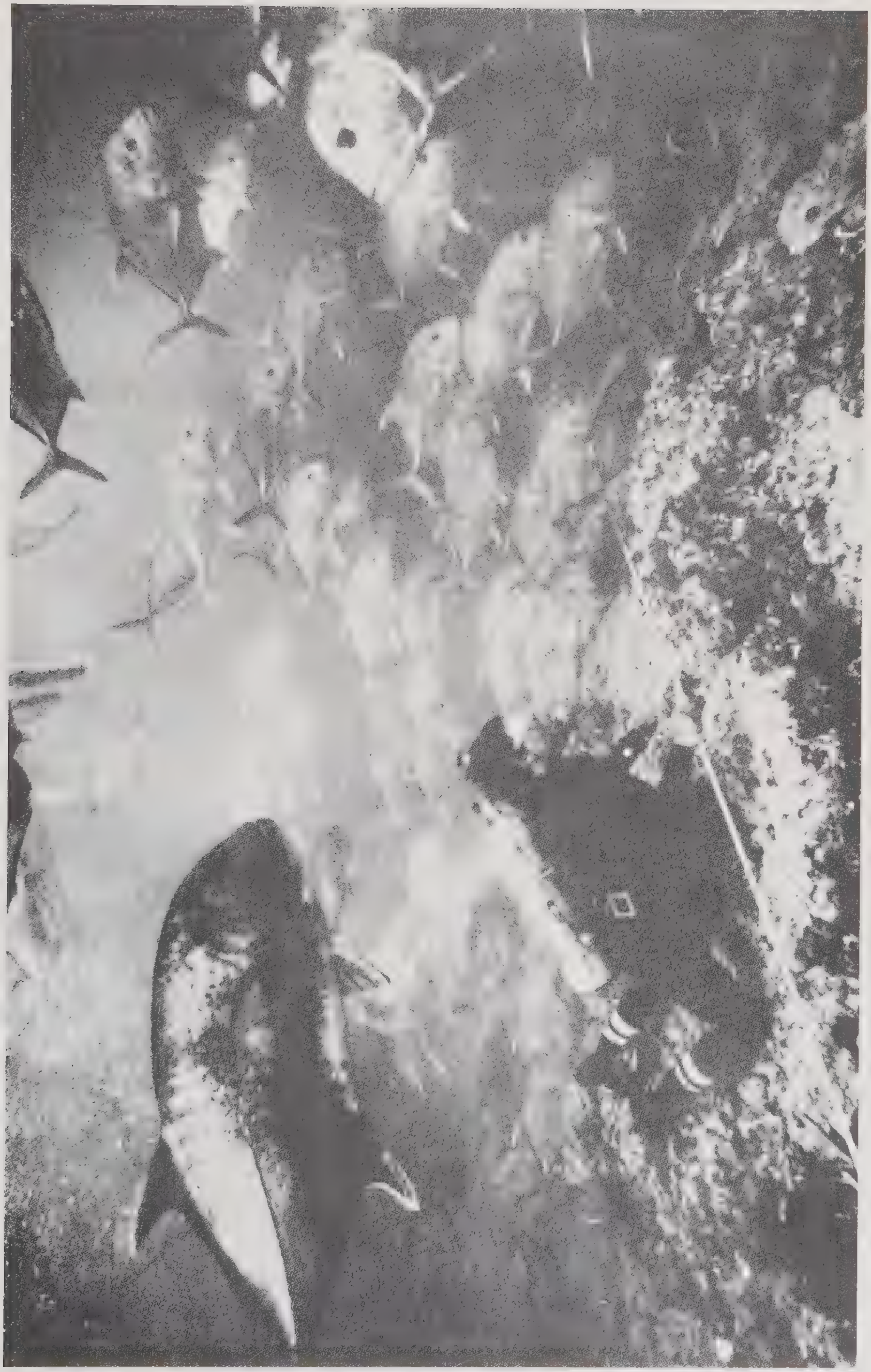

Figure 2. *Caranx ignobilis* at Maro Reef

were the pentacerotid *Hystiopterus acutirostris* and the pomacanthid *Genicanthus personatus*, neither of which were seen elsewhere during this study period.

In comparison, consider the many more species that occurred in two or more transects in any one habitat in the lee of the island of Hawaii, but were not seen at Kure or Midway (Table 5). Three -- *Chromis agilis*, *Plectroglyphidodon imparipennis*, and *Acanthurus nigrofuscus* -- were among the major species noted above. Five -- *Chaetodon reticuluatus*, *C. lineolatus*, *Hemitaurichthys thompsoni*, *Forcipiger longirostris*, and *Ostracion whitelyi* -- were seen nowhere else, while four -- *Epinephelus argus*, *Chaetodon ephippium*, *Plectroglyphidodon sindonis*, and *Pervagor melanocephalus* -- occurred northward only in sharply reduced numbers. Two -- *Thalassoma quinquevittata* and *Ctenochaetus hawaiiensis* -- occurred only in the lee of Hawaii and at French Frigate Shoals. The remaining 11 species in this group -- *Aphareus furcatus*, *Monotaxis grandoculis*, *Coris gaimard*, *Thalassoma fuscus*, *Scarus rubrovilaceus*, *Naso lituratus*, *N. breviorstris*, *Plagiotremus goslinei*, *Rhinecanthus rectangulus*, *Cantherines sandwichiensis*, and *Canthigaster amboinensis* -- were relatively numerous as far as French Frigate Shoals, or Gardner Pinnacles, but declined sharply in numbers northward from there.

Perhaps the most striking departure from the general patterns of distribution outlined above was the almost total absence of small planktivorous fishes at Lisianski and adjoining Neva Shoal (data from the two locations are combined in Table 3). Not only were there no planktivores in the transects at these locations, but the only ones seen in all the widespread observations there were just a few scattered *Chromis ovalis*. At these same locations, on the other hand, the monacanthid *Pervagor spilosoma* was unusually abundant. It may be significant that most of the *P. spilosoma* were found above the reefs in small aggregations, much like those formed by the planktivorous *Chromis* spp. elsewhere, rather than scattered close to the reef as members of this species usually are. These same circumstances were paired at Kahe, on leeward Oahu, where in two transects conducted 4 months apart planktivores were absent, and *P. spilosoma* represented 4.6 and 5.6 percent of the fishes counted (compared with a mean of 0.5 percent; range 0 to 0.9 percent in transects elsewhere off leeward Oahu). Interestingly, the transects at Lisianski (and Neva Shoal) and at Kahe were the only ones during the entire study (in water more than 2 m deep) in which planktivores were absent (where in fact at least one planktivorous species was not a major form) and in which *P. spilosoma* represented more than 1 percent of the fishes present.

In all of the widespread locations visited during this study, only three species were seen that did not also occur either off the island of Hawaii or at Midway-Kure. Two of these -- the chaetodontids *Chaetodon trifasciatus* and *C. citrinellus* -- occurred only at French Frigate Shoals, whereas the monacanthid *Cantherines verecundes* occurred only at Laysan and Lisianski.

TABLE 5. OCCURRENCES OF SPECIES COUNTED IN TWO OR MORE TRANSECTS IN ANY ONE HABITAT MOVING NORTHWESTWARD IN THE HAWAIIAN ARCHIPELAGO

Species	Location[1]														
	Hl	Hw	Ol	Ow	NU	NI	NE	FFS	GP	MR	LA	LI	PH	MI	KA
Epinephelus argus	*				*										
Aphareus furcatus	*	*	*		*	●		x	●	x					
Monotaxis grandoculis	*	x	●		x	x	●	x			●				
Chaetodon ephippium	*				●	x									
C. reticulatus	*														
C. lineolatus	*														
Forcipiger longirostris	*														
Hemitaurichthys thompsoni	*														
Chromis agilis	*	x	x					x							
Plectroglyphidodon imparipennis	*	x	●	*	●	*	x	*	*						
P. sindonis	*	●						●	x						
Coris gaimard	*	x	x	●		●	*	x							
Thalassoma fuscus[2]	*	●	●	●	●	●	●	x	●	●					
T. quinquevittata	*							x							
Scarus rubroviolaceus	*	*	x	●	x	●	●	x							
Acanthurus nigrofuscus	*	*	*	*	*	*	x	*	x	x	●				
Ctenochaetus hawaiiensis	*							●							
Naso lituratus	*	*	*	*		*	x	*	x	●		●	●		
N. brevirostris	*				●		x	*	●						
Plagiotremus goslinei	*	*		x	x	x	x		x						
Rhinecanthus rectangulus	*	●	*	x		*	●	●	●		●				
Cantherines sandwichiensis	*	x	*	*	x	*	●	x	x						
Pervagor melanocephalus	*		*	x											
Ostracion whitelyi	*														
Canthigaster amboinensis	*	*	*	*		x		●							

Note: * = occurring in two or more transects; x = occurring in one transect; ● = seen.

[1] Hl = Hawaii: leeward; Hw - Hawaii: windward; Ol = Oahu: leeward; Ow = Ohau: windward; NU = Niihau; NI = Nihoa; NE = Necker Island; FFS = French Frigate Shoals; GP = Gardner Pinnacles; MR = Maro Reef; LA = Laysan Island; LI = Lisianski Island; PH = Pearl and Hermes Atoll; MI = Midway Islands; KA = Kure Atoll

[2] The nominal T. umbrostigma, which is considered the female of this species based on observations of spawning (Hobson, 1974), was numerous throughout the archipelago.

Chaetodon trifasciatus invariably occurred with coral of the genus *Acropora*, which dominated some reefs at French Frigate Shoals, but was not abundant elsewhere (see paper in this proceedings by Grigg). It was present on all four transect reefs rich in *Acropora*, where it represented a mean of 2.1 percent (range of 1.6 to 3.4 percent) of the fishes counted. *Chaetodon cintrinellus* was relatively abundant in the shallow waters behind the windward reef flat, but no transects were established in that habitat. *Cantherines verecundes* was seen in just one transect at Laysan that was set on a large patch reef at a depth of 20 m, but it represented 3.1 percent of the individuals there. At Lisianski, *C. verecundes* was in all the habitats sampled and represented a mean of 2.7 percent (range of 2.3 to 3.6 percent) of the fishes in the five transects conducted there.

An additional feature of fish communities in the Northwestern Hawaiian Islands was the relatively high incidence in shallow water of the large terminal male phase of many labrid species. Most prominent were: *Bodianus bilunulatus*, *Coris flavovittata*, *Anampses cuvier*, *Thalassoma purpureum*, and *T. ballieui*. These were especially numerous at Midway and Kure.

DISCUSSION

Temporal Stability

The question of whether reef fish communities are stable or unstable over time has evoked much interest in recent years (e.g., Sale, 1980b). Probably it is significant that proponents of the instability concept have based most of their arguments on short-term studies of small isolated reefs. Most have been experimental colonizations of isolated coral heads (e.g., Sale and Dybdahl, 1975) or artificial reefs (e.g., Talbot et al., 1978; Bohnsack and Talbot, 1980) over periods of less than 3 years. The proponents of the stability concept, on the other hand, have drawn most of their evidence from long-term studies of larger reefs. These have included studies of both natural (Brock et al., 1979) and artificial (Ogden and Ebersole, 1981) reefs that were examined more than 10 years after being defaunated and recolonized. A persistent uncertainty in these studies stems from not knowing how long it takes reef communities to fully recover from defaunation. The uncertainty is increased when artificial reefs are involved because no one knows whether these will in fact ever support truly natural communities. Significantly, however, Sale (1980a) found that the structure of fish communities on undisturbed natural, but small (20 m x 1 m x 1 m), patch reefs (which were controls for his defaunation experiments) changed continuously over time.

The major components of the Hawaiian fish communities described in this paper were stable over the duration of the study, and probably it is significant that these communities were established on extensive, natural reefs that had not been disturbed. Based on these circumstances and the variable results noted above, the stability-instability controversy may stem from (1) differences in the size and complexity of the reef systems studied by the various investigators; (2) time passed since the communities had been disturbed; and (3) the extent to which the physical conditions of the reefs approximate those of natural, undisturbed reefs in the area. Also, it is important that the stability reported here refers to the adult populations. As mentioned in the "Methods" section, the numbers of juveniles varied with season and from year-to-year for reasons that seemed unrelated to circumstances on the reef, but this variability had no observable impact on the established adults during this study.

Spatial Distribution: General

Most Hawaiian reef fishes are widely distributed on the islands of the Pacific plate, which occupies most of the Pacific basin, and has been defined by Springer (1982) as a distinct biogeographic unit. Apparently these species are adapted to certain features held in common by the variety of high islands, low islands, atolls, and submerged sea mounts, that characterize this, the largest of the earth's lithospheric plates. It is not surprising, therefore, that so many of them occur in diverse habitats throughout the Hawaiian Archipelago. Despite these widespread occurrences, however, the major species differ greatly in their relative numbers from one habitat to another.

Because most of these major forms were most numerous at one end of the archipelago or the other, it is convenient to focus on the northwestward distribution of the southeastern dominants and the southeastward distribution of the northwestern dominants. Significantly, those species which dominated in the southeast were more restricted in their distribution over the archipelago than were those which dominated in the northwest. Apparently the southeastern dominants -- *Chaetodon multicinctus*, *Plectroglyphidodon imparipennis*, *Chromis agilis*, *C. vanderbilti*, *Acanthurus nigrofuscus*, *Chaetodon strigosus*, and *Zebrasoma flavescens* -- are less attuned to the overall Hawaiian environment than are their northwestern counterparts -- *Myripristis amaenus*, *Kyphosus bigibbus*, *Chromis ovalis*, *Dascyllus albisella*, *Stegastes fasciolatus*, *Thalassoma duperrey*, *T. ballieui*, *Acanthurus leucopareius*, *A. nigroris*, and *A. triostegus* (Table 3). Not only are the southeastern dominants less numerous in more places throughout the archipelago, but they also include fewer endemics -- just one (*C. multicinctus*) compared with four (*C. ovalis*, *D. albisella*, *T. duperrey*, and *T. ballieui*) among the northern groups. It is recognized that some of the most abundant Hawaiian species are endemics (Gosline and Brock, 1960), but not all of the endemics are abundant (e.g., the pomacentrid *Plectroglyphidodon sindonis*, Table 5).

Patterns of distribution northwestward are basically different from patterns of distribution southeastward presumably because of different selection pressures. In the discussion below several of these selection pressures are distinguished.

Environmental Selection Pressures That Influence Distribution Northwestward

The species in nearshore communities at the southeastern end of the archipelago show close relationships with the fishes of the more tropical regions of the Pacific. Even the one endemic species among the major forms -- *Chaetodon multicinctus* -- has a western Pacific analog in *C. punctatofasciatus*, and a South Pacific analog in *C. pelewensis* (Burgess, 1978). The several species that occurred in transects in the lee of the island of Hawaii, but were not seen elsewhere (Table 5) -- *Chaetodon reticulatus*, *C. lineolatus*, *Hemitaurichthys thompsoni*, *Forcipiger longirostris*, and *Ostracion whitelyi* -- are widespread Pacific species that apparently find conditions more suitable here than elsewhere in Hawaii. Gosline and Brock (1960) reported that *C. reticulatus* has been "reported only twice in Hawaii," that *C. lineolatus* inhabits "relatively deep water," and that *H. thompsoni* is "quite rare." They included *O. whitelyi* (as *O. solorensis*) in their account of the Hawaiian fauna based only on a small specimen from Johnston Island, but Randall (1972) subsequently noted its occurrence in the lee of Hawaii. *F. longirostris* was long confused with the common *F. flavissimus*, but now is recognized as a distinct species rare in the Hawaiian Archipelago except on the leeward reefs of the island of Hawaii (Randall and Caldwell, 1970). *Chromis agilis* is common and widespread in the tropical western Pacific (Allen, 1975) but has a limited distribution in Hawaii. Although it is the major species on certain reefs in the lee of Hawaii where the coral *Porites compressa* is abundant, its occurrence northwestward is limited to small aggregations off windward Hawaii and leeward Oahu (on a reef in Hanauma Bay which is rich in *Porites compressa*). One individual was seen at French Frigate Shoals.

One might assume that distribution of tropical Pacific fishes northwestward in the Hawaiian Archipelago would be limited by lower water temperature. This is probably true for some species, but certain other forces are more limiting for other species.

Reduced protection from prevailing wind and seas northwestward probably limits distribution for some species. *Zebrasoma flavescens*, for example, seemed to require some feature associated with leeward reefs. This species is the major component of communities on various reefs in the lee of Hawaii, the largest island, but is much less prominent in the lee of the smaller island of Oahu. On the windward side of Hawaii, adults were seen in numbers only south of Cape Kumukahi, where there is in essence a lee shore. North of the cape along the Hamakua Coast just one adult occurred in the transects, whereas juveniles were the most numerous fish on a reef rich in the coral *Porites compressa* in a sheltered bay near Hilo. Conditions suitable for adults were clearly lacking along the Hamakua Coast, however, as only a few were seen.

Zebrasoma flavescens was found to be sparse off windward Oahu, except in Kaneohe Bay. This pattern is consistent with the work of Brock (1954), who found this fish to be prominent only in certain leeward habitats around Oahu and Hawaii. *Zebrasoma flavescens* was sparsely distributed in the Northwestern Hawaiian Islands during this study, generally as a few individuals on the more protected reefs. The only sightings at Midway, for example, were a few scattered individuals on patch reefs in the lagoon where the coral *Porites compressa* also was most abundant. Apparently this coral, which grows as closely spaced finger-like branchings, is important to the juveniles of *Z. flavescens*, just as it appears to be for adult *Chromis agilis*.

The decreased occurrence of exposed basalt northwestward appeared to influence the distribution of several species, most notably *Acanthurus nigrofuscus*, which Randall (1960) described as "...probably second only to the manini (*Acanthurus triostegus*) in abundance among surgeonfishes in Hawaii." This species was numerous only where the reefs were largely exposed basalt, a widespread habitat in the high islands. The dependence of *A. nigrofuscus* on some factor related to exposed basalt was especially evident at French Frigate Shoals, where its prominence was confined to La Perouse Pinnacle, the only basaltic structure there. At Gardner Pinnacles, the last exposed basalt occurrence northwestward, *A. nigrofuscus* was numerous on the basaltic face of the pinnacles, but was not seen elsewhere. Only one individual was seen at Maro Reef and another at Laysan, the latter in a transect. None were seen northwestward from there. Despite the apparent dependence of Hawaiian *A. nigrofuscus* on habitats that include exposed basalt, the occurrences of this species, on Pacific atolls (Randall, 1956), which lack such habitats, indicates that conspecifics elsewhere may have different requirements. The same is true of the pomacentrid *Plectroglyphidodon imparipennis*, which was found only among surge-swept basaltic reefs during this study (it was not seen northwest of Gardner Pinnacles), but is widespread elsewhere in the Pacific on reefs that lack exposed basalt (Allen, 1975). Three other species with distributions that coincided with exposed basalt were Hawaiian endemics: the pomacentrid *Plectroglyphidodon sindonis* (which frequented surge-swept boulders), the blenniid *Plagiotremus goslinei*, and the monacanthid *Cantherines sandwichiensis*.

Certain species which are widespread in the central Pacific seem to find conditions more suitable at French Frigate Shoals than elsewhere in the Hawaiian Archipelago. Probably the most striking example is the common occurrence of the chaetodontid *Chaetodon trifasciatus*, a species that lives in close association with corals of the genus *Acropora* (Burgess, 1978). Both the fish and corals are common throughout most of the tropical Indo-Pacific, but are rare or absent in the Hawaiian Archipelago except at French Frigate Shoals. In noting the abundance of *Acropora* at French Frigate Shoals and its sharp decline both southward (to Kauai) and northward (to Laysan), Grigg et al. (1981) suggested that French Frigate Shoals is the site of active colonization of some Indo-Pacific forms from the west (by way of the subtropical countercurrent), and that this location is the center of distribution of such forms to the other islands. This pattern is consistent with the distribution of some Indo-Pacific fishes in Hawaii. Another widespread Indo-Pacific species that was abundant at French Frigate Shoals, but which went unseen elsewhere during this study, was the chaetodontid *Chaetodon citrinellus*. This species, considered rare in Hawaii by Gosline and Brock (1960), was among the species that colonized a newly created harbor on the lee shore of Hawaii (Brock, 1981).

These two widely separated and very different settings -- French Frigate Shoals and leeward Hawaii -- may have characteristics that make them more suitable than other Hawaiian habitats for certain Indo-Pacific species. Leeward Hawaii is noted for its warm, sediment-free water and rich coral growth -- all of which are likely to be associated with environments favored by fishes adapted to more tropical Pacific habitats. French Frigate Shoals may be favorable to some because it is in essence a barrier reef that encloses expansive shallows -- a setting which is widespread in the more tropical areas of the central and western Pacific, but limited in those islands to the southeast of French Frigate Shoals.

Barrier reefs that enclose expansive shallows are prominent to the northwest of French Frigate Shoals, especially at Pearl and Hermes, Midway, and Kure -- which are atolls. But during the winter water temperatures fall below 18 C at these locations (Mauck, 1975) which presumably would be a problem for many Indo-Pacific species. Water temperature, however, has not limited *Epibulus insidiator*, a widespread Indo-Pacific labrid that is common from French Frigate Shoals northwestward to Kure, but which has not been reported southeastward to Hawaii.

Environmental Selection Pressures that Influence Distribution Southeastward

Although the major species in the northwestern communities are more distinctively Hawaiian than their southeastern counterparts, they too are closely related to fishes of the tropical western Pacific. But some of the less prominent species in the northwest are closely related to, or conspecific with, fishes of the more temperate regions in the western Pacific. Furthermore, in contrast with the major species in these communities, which are widely distributed in shallow water, these more temperate species have limited distributions on shallow reefs southeastward. Both *Opelgnathus fasciatus* and *O. punctatus* are prominent in coastal waters of Japan, where they are popular game fishes (Masuda et al., 1975). But despite the common occurrences of both species at Kure and Midway, they are uncommon elsewhere in the Hawaiian Archipelago. *O. punctatus* had not been recorded from Hawaii prior to this study (Hobson, 1980), and *O. fasciatus* was recognized from just one specimen taken almost a century ago (Gosline and Brock, 1960).

Similar relationships to fishes of more temperate regions in the western Pacific exist for *Pristolepis oligolepis*, *Pseudocaranx dentex*, *Cheilodactylus vittatus*, and *Histiopterus acutirostris*, all of which also occur in Japanese waters (Masuda et al., 1975; Springer 1982). But here another dimension of distribution must be considered -- variations in depth of occurrence with latitude. All four species are common inhabitants of shallow reefs at Kure and Midway, but occur at greater depths southeastward. Gosline and Brock (1960) noted that although *H. acutirostris* appears to be rare there, *P. oligolepis* and *C. vittatus* are not uncommon in deeper water. *P. dentex* (as *Caranx cheilio*), according to Gosline and Brock, is "not now common around the high islands, but is abundant from French Frigate Shoals to Midway," and Moffitt (1980) reported it to be a major target of offshore bottom fishermen in the Northwestern Hawaiian Islands.

Many fishes which have wide latitude distribution inhabit deeper water toward the equator (Hubbs, 1948). The distribution of such fishes often relates to water temperatures, as shown by studies along the western coast of North America where the pattern reverses at points of local upwelling (Hubbs 1948). Thus, at least some of the fishes that inhabit progressively deeper habitats southeastward in Hawaii may be responding to features related to water temperature. In addition to the species mentioned above, an affinity to lower water temperatures may account for the distribution of *Genicanthus personatus*, which is relatively common on reefs 20 to 30 m deep at Midway and Kure, but which has been reported only from deeper water around the high islands (Randall, 1975). The same pattern may hold true for the grouper *Epinephelus quernus*, which is common on shallow reefs at Midway and Kure, but is only found in deeper water southeastward. This species constitutes a large part of the catch of the offshore hand-line fishery at depths below 60 m around the high islands (Ralston, 1980). The same pattern may hold true for the large terminal male phase of the labrid *Bodianus bilunulatus*, which is another form that commonly frequents reefs as shallow as 1 m at the northwestern end of the archipelago, but rarely occurs shallower than 20 m at the southeastern end.

Pristolepis oligolepis, *P. dentex*, *C. vittatus*, and *H. acutirostris*, as well as certain congeners of *G. personatus*, *B. bilunulatus*, and the two oplegnathids, have antitropical distributions that are thought to have been established when surface waters were cooler than at present (Randall, 1981). Springer (1982), however, cited evidence that equatorial sea-surface temperatures have been relatively stable since these antitropical distributions are thought to have been established. He suggested that these distributions have an ecological basis related to the antitropical distribution of the high islands, but this possibility is inconsistent with the fact that most of the species involved are more numerous around the Hawaiian atolls than around the high islands.

The Planktivore-*Pervagor spilosoma* Anomaly

The possibility of a connection between an absence of planktivores and an abundance of *Pervagor spilosoma*, is strengthened by the fact that at the only locations where either circumstance occurred -- Lisianski (and Neva Shoal) and Kahe, Oahu -- they occurred together. The basis for the apparent relationship between these species, or between these species and the two locations, remains unclear. Perhaps it is significant that the water at Lisianski was noted to have a milky quality and that a fine sediment coated much of the seafloor, especially at Neva Shoal. This condition can mean that the water is not circulating, which would in turn mean a reduced supply of zooplankton. On the other hand, it is conceivable that certain materials in suspension could adversely affect small planktivores. There is no measure of the zooplankton at these locations, but it was striking that in the absence of planktivores at Lisianski, the normally bottom-dwelling *P. spilosoma* aggregated above the reef, just as the planktivores did elsewhere. These *S. spilosoma* were not seen feeding, however, and a diet of zooplankters certainly would have been a radical departure from the usual diet of this species. Under more typical circumstances at the island of Hawaii, *P. spilosoma* fed primarily on scleractinian coral polyps (Hobson, 1974). On the other hand, it is conceivable that under appropriate circumstances, features adapted to pluck coral polyps could also be effective in feeding on zooplankters.

Fishing Pressures

Because fishing pressures have been concentrated on just certain places, they seem likely to have distorted patterns of distribution for at least some species. Fishing pressures seem to account for the reduced numbers in the southeast of certain of the species prominent in the northwest (Tables 3 and 4). Perhaps this was predictable, because fishing pressures should have been expected to increase toward the fishing ports on the major high islands. Nevertheless, it is difficult to hold fishing pressures accountable for the southeastward decline of some species. Although *Epinephelus quernus* and *Pseudocaranx dentex* are major targets of fishermen in the area southeast of Midway, the fishing effort is in deeper water offshore. There has been virtually no fishing on the shallow reefs of the Northwestern Hawaiian Islands from Pearl and Hermes Atoll southeastward; hence, the absence of *E. quernes* and *P. dentex* from these reefs cannot be attributed to fishing pressures. Probably both species are simply better adapted to deeper water in southeastern areas.

Population shifts into deeper water cannot account for the southeastward decline in numbers of some shallow-water potential target species. This is because they inhabit shallow reef areas throughout the archipelago. Some of those which are abundant throughout the Northwestern Hawaiian Islands, but generally sparse throughout the major high islands, such as the shark

Carcharhinus amblyrhynchos, may find certain environmental features of major high island reefs unfavorable. On the other hand, shark populations are known to be particularly vulnerable to fishing pressures, and there have been concerted and apparently successful efforts to reduce the populations of these fishes around the high islands.

The most likely victims of fishing pressures are those species known to be well adapted to shallow-water reef areas in the high islands, but which were found only in low numbers during this study. Examples among the species listed in the tables are the holocentrid *Myripristis amaenus* and the carangid *Caranx ignobilis*. *M. amaenus* and its congeners *M. murdjan* and *M. kuntee*, are prime targets of fishermen and are especially vulnerable owing to their habit of concentrating in reef caves during the day. [*M. kuntee* was considered a major species in the preliminary report on this study (Hobson, 1980) based on its numbers in one transect in the lagoon at Kure atoll.] *C. ignobilis* is coveted by both spearfishermen and shore fishermen and is especially vulnerable to the former owing to its boldness. Fishing would seem to have had a major influence on the observed distribution of *C. ignobilis*. In contrast to its extreme prominence from Nihoa northwestward to Kure, it was never observed in the major high islands during this study. On other occasions in the high islands, sightings have been infrequent and usually involved solitary individuals.

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CIGUATERA AND THE FEEDING HABITS OF THE GREATER AMBERJACK, *SERIOLA DUMERILI*, IN THE HAWAIIAN ARCHIPELAGO

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ABSTRACT

Stomach contents collected from those greater amberjack, *Seriola dumerili*, tested for ciguatoxicity, were (1) examined to determine whether a relationship exists between feeding habits and incidence of toxicity, and (2) analyzed to determine the extent of geographic variability in the diet. Amberjack were classified into two weight groups. Large fish caught in the main Hawaiian islands fed predominantly on *Decapterus* regardless of their level of ciguatoxicity. For small amberjack, *Decap-terus* again predominated in the diet with these exceptions: those determined as being ciguatoxic and those caught in the Northwestern Hawaiian Islands. These two groups, plus the large nonciguatoxic amberjack of the Northwestern Hawaiian Islands fed more on bottom-associated fauna than all other groups studied. A series of hypotheses were generated from these results to explain the observed dietary differences.

ciguatera Hawaiian Archipelago
amberjack feeding habits

INTRODUCTION

Ciguatera is a toxin-related malady caused by the consumption of certain reef fishes of the tropics and subtropics. The symptoms include a variety of gastrointestinal and neurological disorders which occasionally cause death. The reef fishes involved are primarily algal and detrital feeders and higher reef predators, including some neritic predators which range into the reef environment. Virtually no evidence of toxicity exists for reef planktivores and pelagic fishes (Withers, 1982).

A source of the toxic agent, ciguatoxin, has been identified as a benthic dinoflagellate, *Gambierdiscus toxicus*, from surveys conducted by Yasumoto et al. (1977a, 1977b) of reef areas around the Gambier Islands, French Polynesia. This dinoflagellate has also been identified from Oahu, Hawaii by Taylor (1979) and found to be toxicologically similar to the Gambier Islands population (Shimizu et al., 1982).

The linkage of ciguatoxin production to *G. toxicus* supports a theory proposed by Randall (1958) which, in part, suggests that the toxin originates in the benthic reef environment. Additionally, Randall (1958) suggests that the toxin is transmitted via the food chain to fishes of higher trophic levels. The latter is supported by identification of the dinoflagellate among the gut contents of a ciguatoxic acanthurid, *Naso unicornis*, from studies by Yasumoto et al. (1977a). Although this is the only such finding to date, studies on two ciguatoxic acanthurids, *Ctenochaetus strigatus* and *Acanthurus lineatus* (Yasumoto et al., 1971), and on the ciguatoxic scarid, *Scarus gibbus* (Yasumoto et al., 1977c), revealed gut contents containing ciguatoxin. These species all belong to the lower reef trophic levels and are herbivores or detrital feeders. Fishes at these trophic levels are considered the initial accumulators of ciguatoxin; later, as prey they transmit the toxin to fishes in higher trophic levels. This pattern of transmission agrees well with documented accounts of a ciguatera outbreak at Hao Atoll, Tuamotus in 1966-68 (Banner, 1976).

Among the higher reef predators prone to be ciguatoxic is the amberjack, *Seriola dumerili*, whose distribution is worldwide in tropical and subtropical waters. In Hawaii, amberjack is found throughout the archipelago in the inner reef and outer reef slope environments. The adults are primarily found near the bottom, although they are capable of considerable vertical mobility ranging from the surface to depths of 240 m.

Dietary studies on amberjack are few and do not include any from Hawaii. Valdes-Munoz (1980) examined the stomachs (9 empty) of 21 amberjack from Cuban waters as part of a food study on 6 species implicated in ciguatera poisonings. The pomadasyid, *Haemulon sciurus*, and lutjanid, *Lutjanus synagris*, occurred most frequently in the stomachs. Randall (1967) examined 8 stomachs (2 empty) from the West Indies and found only fish as prey items including *Calamus* sp., *Caranx ruber*, *H. aurolineatum*, and *Priacanthus arenatus*. In a study of the biology and fishery of amberjack in southern Florida, Burch (1979) described the contents of 135 stomachs. Prey items occurring most frequently were lutjanids, carangids, portunids, and loligids.

Since these studies did not determine ciguatoxin levels in the amberjack sampled, little information is available on the identity of the prey species involved in ciguatoxin transmission. The opportunity to conduct such a study in Hawaii arose after a 1979 outbreak of ciguatera which implicated amberjack. This incident, coupled with previously reported cases from Hawaii and adjacent Pacific areas (Kubota, 1981) and amberjack's commercial importance in Hawaii, led to the initiation of a ciguatoxin testing program.

In this program -- involving the Southwest Fisheries Center Honolulu Laboratory of the National Marine Fisheries Service, the fishing industry, the University of Hawaii Department of Pathology, and state agencies -- flesh samples were tested for ciguatoxin levels from all amberjack delivered for sale to the United Fishing Agency (UFA) fish auction in Honolulu. Concurrently, an investigation was begun into possible dietary differences between the ciguatoxic (CTC) and non-ciguatoxic (non-CTC) amberjack. This report also includes geographical dietary comparisons among non-CTC amberjack.

METHODS

Weight, fork length, sex, and usually catch location were recorded for amberjack samples at the UFA fish auction. Only fish caught in the fishery around Penguin Bank, Kahoolawe, Lanai, Maui, and Hawaii in the lower main Hawaiian islands (LMHI) and those caught from Gardner Pinnacles to Necker bank in the Northwestern Hawaiian Islands (NWHI) were examined. These two general areas are separated by some 645 km (Figure 1). Commercial amberjack fishing was conducted primarily in depths ranging from 55 to 110 m in both areas.

Flesh samples were tested for ciguatoxin at the University of Hawaii John A. Burns School of Medicine, Pathology Department, by a radioimmunoassay (RIA) technique (Hokama et al., 1977). The toxicity levels of the fish tissues were determined from gamma radiation counts per minute per gram tissue (cpm/g) and were classified as follows: <350,000 cpm/g tissue -- negative; 350,000 to 399,999 cpm/g tissue -- borderline; and ≥400,000 cpm/g tissue -- positive. All borderline cases were considered ciguatoxic.

Stomachs from CTC and non-CTC amberjack caught in the LMHI were collected during February 1980 to February 1981 and July 1979 to March 1980, respectively. Samples from non-CTC amberjack in the NWHI were collected during June to July 1979 and June to October 1980. No stomach samples of CTC amberjack from the NWHI were available.

Stomachs were sampled and preserved in 10 percent Formalin at the auction market. Because there was a lapse of 1 to 10 days between capture and the time the fish were brought to auction, the condition of stomach contents was often poor.

In the laboratory, stomach contents were sorted into identifiable groups. Stomachs containing only unidentifiable remains were discarded and not utilized in the study. Bait could be identified by its appearance and state of digestion. Bait and

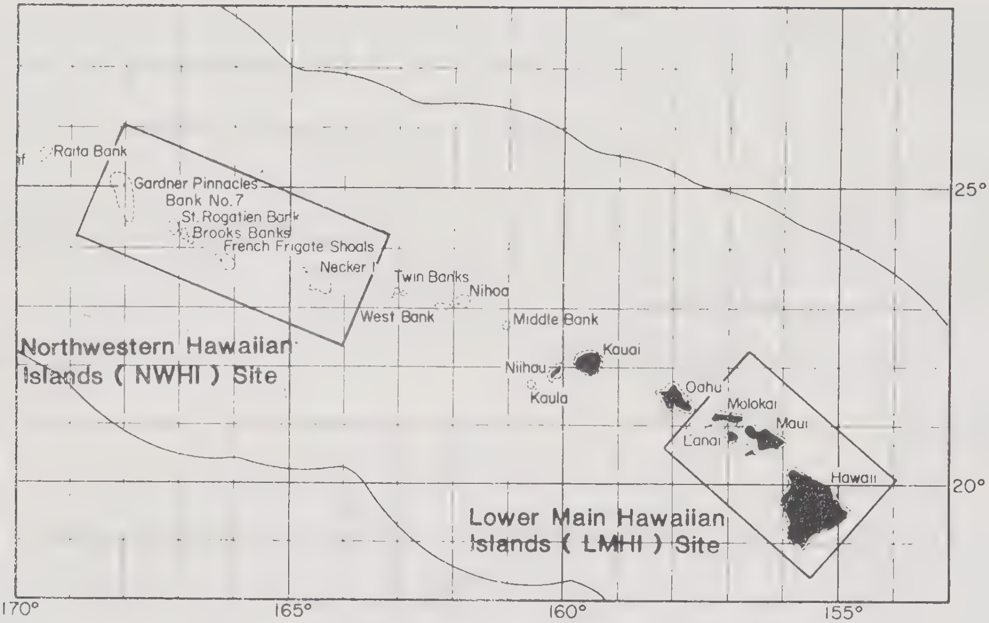
Raita Bank
Gardner Pinnacles
Bank No.7
St. Rogatien Bank
Brooks Banks
French Frigate Shoals
Necker I
Twin Banks
Nihoa
West Bank
Middle Bank
Kauai
Niihau
Kaula
Oahu
Molokai
Maui
Lanai
Hawaii
Northwestern Hawaiian Islands (NWHI) Site
Lower Main Hawaiian Islands (LMHI) Site
25°
20°
170°
165°
160°
155°

Figure 1. The two study areas of the fishery for amberjack in the Hawaiian Archipelago

parasites were recorded but not considered as food items. The volume of each food item was measured by water displacement.

Prey items were identified to lowest possible taxon. Invertebrates were digested rapidly, and frequently could be identified only to suborder. Fishes were usually identifiable to family and sometimes to species. Exceptions were the eels and flatfishes which were only identified to order. Fish in an advanced state of digestion were cleaned of flesh, stained in alizarin, and identified by vertebral count and bone morphology.

The total number (N), frequency of occurrence (F), and aggregate total volume (V) were converted to percentages to the nearest 0.1 percent for all prey taxa, and the index of relative importance (IRI) (Pinkas et al., 1971) was computed as follows:

$$IRI = \%F \times (\%N + \%V) .$$

The IRI values were rounded off to the nearest whole number. The IRI's of 0.6 to 0.9 were rounded off to 1 whereas values 0.5 and less were represented as <1. The IRI values ≥ 100 were considered to represent major food items.

Prey comparisons were made among class taxa and the lower identified taxa. Class comparisons offered information on the general animal types in the diet whereas lower taxa comparisons yield more specific information on the prey and diet. Prey identifiable only to class (i.e., unidentified fish, crustaceans, and cephalopods) were treated as separate entities and included in the lower taxa comparisons.

Diet was also analyzed by ecological habitat with respect to available information on the spatial distribution of prey within the Hawaiian Archipelago. The objective was to indirectly determine whether amberjack feed preferentially on bottom or midwater fauna. Three arbitrary categories were used: (1) benthic and demersal, (2) midwater and surface, and (3) combination of both habitats. This latter category includes prey which are known or suspected of inhabiting both environments equally (Natantia) and those which change habitat during larva, juvenile, or adult stage (Mullidae, Zeidae, and Tetraodontidae). Unidentified carangids, cephalopods, crustaceans, and fish were excluded from the habitat comparison.

To reduce the possibility of an artifact in dietary differences due to amberjack size alone, CTC and non-CTC amberjack were divided into two weight groups: 4.00 to 8.99 kg (small) and those >8.99 kg (large). Small amberjack were most commonly encountered during the study. Large amberjack were much less abundant but corresponded to the size commonly thought (in Hawaii) to be more frequently CTC.

RESULTS

A dietary comparison between CTC and non-CTC amberjack was investigated only within the LMHI. Among small amberjack of both these groups, the predominate class taxon in the diet was fish; crustaceans and cephalopods contributed little to the diet (Tables 1 and 2). *Decapterus* spp. were the most important (IRI = 457) among lower taxa in the CTC group. Other major lower taxa were Teuthoidea (IRI = 246), *Symphysanodon maunaloae* (IRI = 232), crustaceans (IRI = 169), Natantia (IRI = 167), Synodontidae (IRI = 139), and Myctophidae (IRI = 118) (Figure 2, Table 1). In the non-CTC group, *Decapterus* spp. were also the greatest contributor (IRI = 2,421) followed by Natantia (IRI = 466) and *S. maunaloae* (IRI = 188) (Figure 3, Table 2).

In the diet of large amberjack, fish again predominated in both CTC and non-CTC groups with minor contributions of crustaceans and cephalopods (Tables 3 and 4). In the CTC group, *Decapterus* spp. dominated (IRI = 1,429) among lower taxa followed by Teuthoidea (IRI = 727), Myctophidae (IRI = 177), and Engraulidae (IRI = 101) (Figure 4, Table 3). In the non-CTC group, *Decapterus* spp. also ranked highest (IRI = 1,894) followed *Auxis thazard* (IRI = 119) (Figure 5, Table 4).

TABLE 1. PREY ITEMS OF SMALL CTC AMBERJACK FROM THE LOWER MAIN HAWAIIAN ISLANDS (N = 88) LISTED IN DECREASING IMPORTANCE BY TAXA. TAXA OF LESSER PREY (THOSE WITH IRI VALUES BELOW 100) ARE LISTED WITH THEIR RESPECTIVE IRI VALUES ONLY.

	%N	%F	%V	IRI
Taxa of prey				
Fishes	44.0	88.6	91.8	12,032
Crustaceans	38.9	29.6	4.6	1,288
Cephalopods	17.1	21.6	3.6	447
Major lower taxa prey				
Decapterus spp.	3.3	13.6	30.3	457
Teuthoidea	14.6	14.8	2.0	246
Symphysanodon maunaloae	9.0	15.9	5.6	232
Crustaceans	10.2	15.9	0.4	169
Natantia	15.1	10.2	1.3	167
Synodontidae	5.9	12.5	5.2	139
Myctophidae	5.4	18.2	1.1	118
Taxa of lesser prey				
Fish				86
Caridea				44
Octopoda				13
Pontinus macrocephala				12
Priacanthidae				12
Pomacentridae				11
Heterocarpus ensifer				8
Lutjanidae				8
Pristipomoides sp.				8
Serranidae				8
Anthias sp.				7
Auxis thazard				7
Labridae				7
Xanthichthys mento				7
Scorpaenidae				5
Mullidae				4
Reptantia				4
Selar crumenophthalmus				4
Carangidae				3
Cephalopod				3
Emmelichthyidae				2
Percophididae				2
Pleuronectiformes				2
Symphysanodon typus				2
Ammodytidae				1
Antigonia steindachneri				1
Chaetodontidae				1
Dactylopteridae				1
Grammatonotus laysanus				1
Munida sp.				1
Penaeidea				1
Plesionika longirostris				1
Plesionika sp.				1
Portunidae				1
Tetraodontidae				1
Anguilliformes				<1
Balistidae				<1
Bleekeria gilli				<1
Congridae				<1
Embolichthys sp.				<1
Engraulidae				<1
Gobiidae				<1
Paguridae				<1
Sphyraenidae				<1

Note: N = total number, F = frequency of occurrence, V = aggregate total volume, IRI = index of relative importance

TABLE 2. PREY ITEMS OF SMALL NON-CTC AMBERJACK FROM THE LOWER MAIN HAWAIIAN ISLANDS (N = 82) LISTED IN DECREASING IMPORTANCE BY TAXA. TAXA OF LESSER PREY (THOSE WITH IRI VALUES BELOW 100) ARE LISTED WITH THEIR RESPECTIVE IRI VALUES ONLY.

	%N	%F	%V	IRI
Taxa of prey				
Fishes	51.2	90.2	95.9	13,268
Crustaceans	43.1	22.0	2.5	1,003
Cephalopods	5.7	20.7	1.6	151
Major lower taxa prey				
Decapterus spp.	6.1	32.9	67.5	2,421
Natantia	40.6	11.0	1.8	466
Symphysanodon maunaloae	10.6	14.6	2.3	188
Taxa of lesser prey				
Teuthoidea	68	*Etelis coruscans*		3
Symphysanodon sp.	56	Bothidae		2
Fish	39	*Heterocarpus ensifer*		2
Pristipomoides sp.	19	Myctophidae		2
Crustaceans	17	Caproidae		1
Synodontidae	16	Caridea		1
Priacanthidae	14	*Decapterus macrosoma*		1
Selar crumenophthalmus	13	Lutjanidae		1
Serranidae	12	Mullidae		1
Engraulidae	10	*Scorpaenopsis* sp.		1
Emmelichthyidae	9	*Symphysanodon typus*		1
Percophididae	9	*Anthias* sp.		<1
Carangidae	8	Labridae		<1
Octopoda	6	Reptantia		<1
Tetraodontidae	6	Scorpaenidae		<1
Cephalopods	4			

Note: N = total number, F = frequency of occurrence, V = aggregate total volume, IRI = index of relative importance

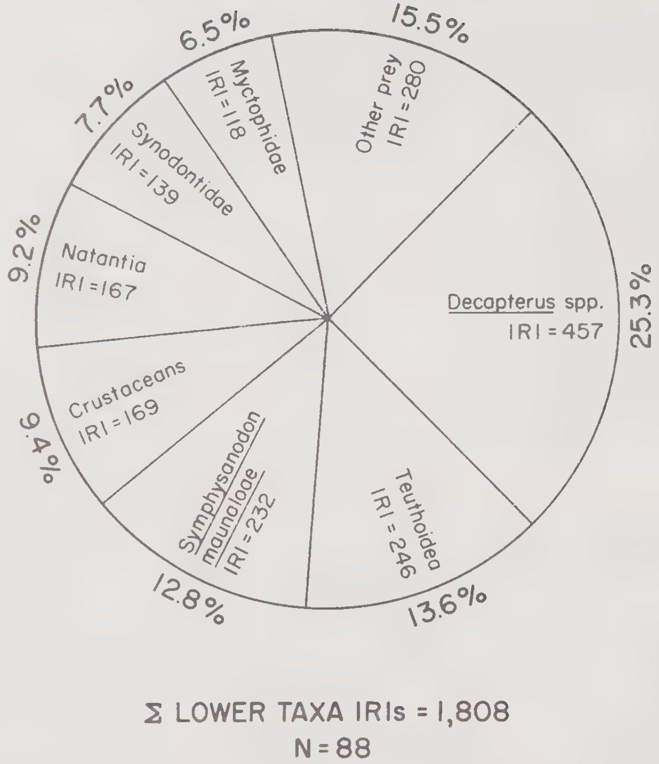

Figure 2. Relative contribution (percent of total IRI) of lower taxa prey in the diet of small CTC amberjack from the LMHI. Taxa of lesser prey are grouped together in the "other prey" category.

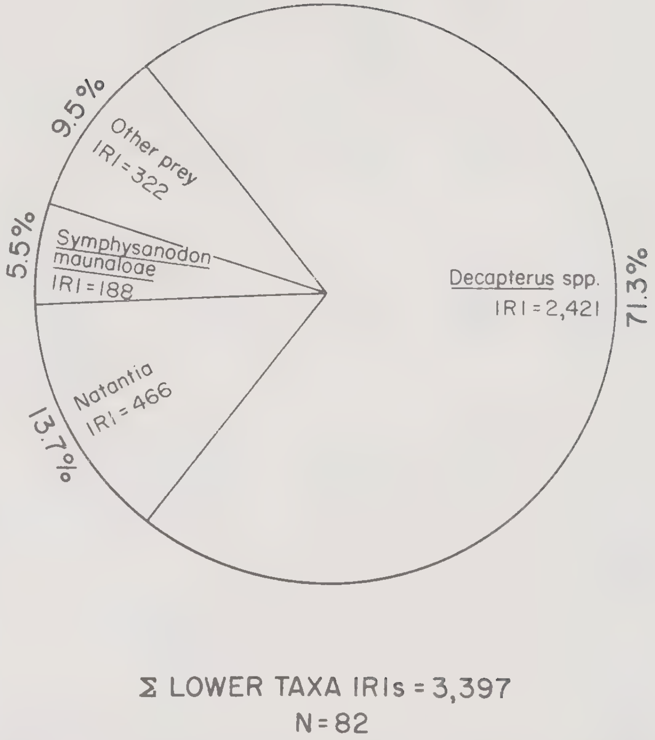

Figure 3. Relative contribution (percent of total IRI) of prey in the diet of small non-CTC amberjack from the LMHI. Taxa of lesser prey are grouped together in the "other prey" category.

TABLE 3. PREY ITEMS OF LARGE CTC AMBERJACK FROM THE LOWER MAIN HAWAIIN ISLANDS (N = 45) LISTED IN DECREASING IMPORTANCE BY TAXA. TAXA OF LESSER PREY (THOSE WITH IRI VALUES BELOW 100) ARE LISTED WITH THEIR RESPECTIVE IRI VALUES ONLY.

	%N	%F	%V	IRI
Taxa of prey				
Fishes	67.3	95.6	98.2	15,822
Cephalopods	29.0	26.7	1.4	812
Crustaceans	3.7	6.7	0.4	27
Major lower taxa prey				
Decapterus spp.	10.5	33.3	32.4	1,429
Teuthoidea	28.4	24.4	1.4	727
Myctophidae	13.0	13.3	0.3	177
Engraulidae	22.2	4.4	0.7	101
Taxa of lesser prey				
Carangidae	73	Natantia		8
Fish	46	Pleuronectiformes		6
Balistidae	37	*Ariomma* sp.		4
Auxis rochei	26	Caridea		3
Mullidae	23	Dactylopteridae		3
Pontinus macrocephala	22	*Auxis* sp.		2
Pristipomoides sieboldii	22	*Decapterus macrosoma*		2
Tetraodontidae	19	*Heterocarpus ensifer*		2
Bothidae	13	Scombridae		2
Auxis thazard	11	Gonostomatidae		1
Priacanthidae	10	Octopoda		1
Fistulariidae	9	Synodontidae		1

Note: N = total number, F = frequency of occurrence, V = aggregate total volume, IRI = index of relative importance

TABLE 4. PREY ITEMS OF LARGE NON-CTC AMBERJACK FROM THE LOWER MAIN HAWAIIAN ISLANDS (N = 53) LISTED IN DECREASING IMPORTANCE BY TAXA. TAXA OF LESSER PREY (THOSE WITH IRI VALUES BELOW 100) ARE LISTED WITH THEIR RESPECTIVE IRI VALUES ONLY.

	%N	%F	%V	IRI
Taxa of prey				
Fishes	59.4	86.8	98.8	13,732
Crustaceans	33.5	20.8	0.5	707
Cephalopods	7.1	11.3	0.7	88
Major lower taxa prey				
Decapterus spp.	14.7	35.8	38.2	1,894
Auxis thazard	2.4	5.7	18.4	119
Taxa of lesser prey				
Lutjanidae	54	Balistidae		5
Myctophidae	54	Caridea		5
Carangidae	52	*Decapterus macrosoma*		5
Natantia	48	*Ariomma* sp.		4
Selar crumenophthalmus	41	Fistulariidae		4
Teuthoidea	41	Tetraodontidae		4
Fish	35	Cephalopods		3
Auxis sp.	32	Polymixiidae		2
Crustaceans	32	*Symphysanodon typus*		2
Reptantia	32	Synodontidae		2
Symphysanodon maunaloae	28	Labridae		1
Heterocarpus ensifer	24	Penaeidea		1
Moridae	10	Amphipoda		<1
Pristipomoides sieboldii	10	Octopoda		<1
Scorpaenidae	9	Paralepididae		<1
Lutjanus sp.	8	*Squilla* sp.		<1
Pristipomoides sp.	8	Triglidae		<1
Scombridae	6			

Note: N = total number, F = frequency of occurrence, V = aggregate total volume, IRI = index of relative importance

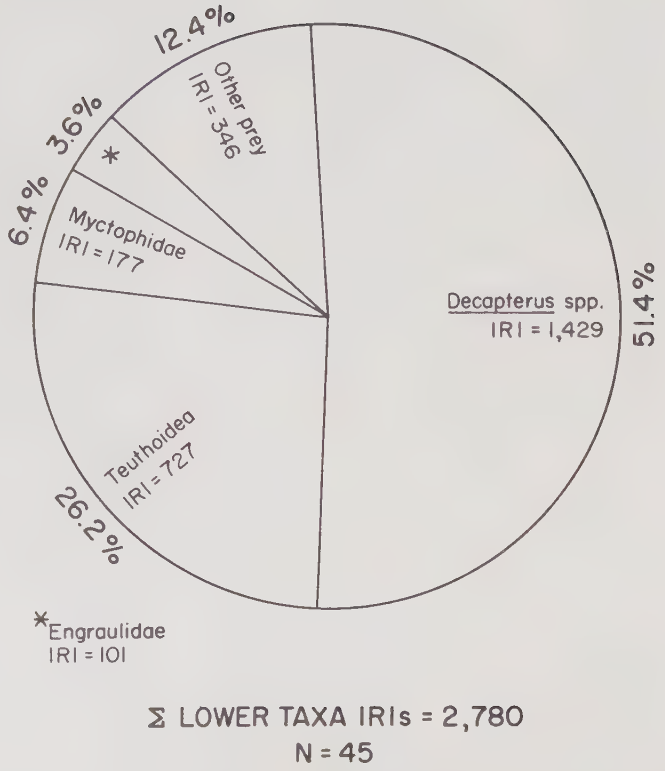

Figure 4. Relative contribution (percent of total IRI) of prey in the diet of large CTC amberjack from the LMHI. Taxa of lesser prey are grouped together in the "other prey" category.

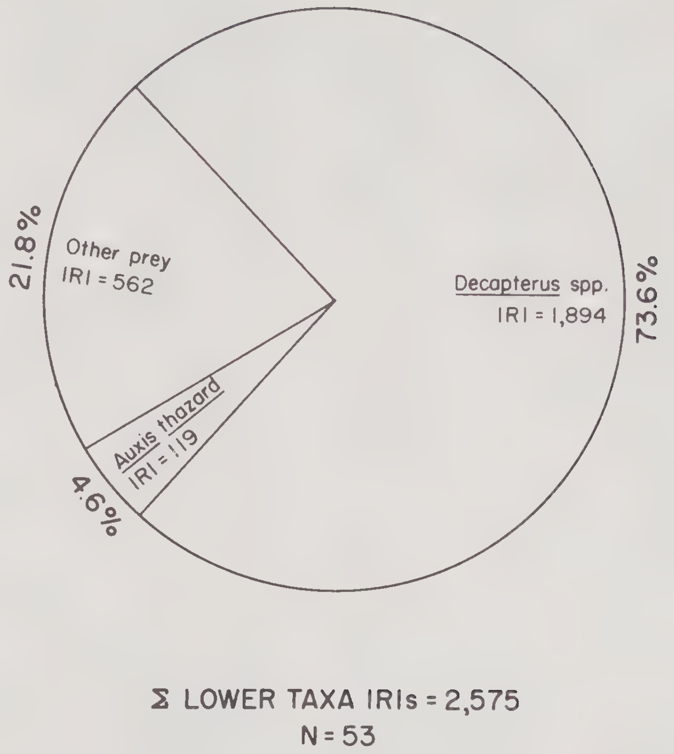

Figure 5. Relative contribution (percent of total IRI) of prey in the diet of large non-CTC amberjack from the LMHI. Taxa of lesser prey are grouped together in the "other prey" category.

The predominance of *Decapterus* spp. were similar, in terms of percentage of total IRI (Figures 3 and 5), in small and large fish of the non-CTC group. Although *Decapterus* spp. ranked highest in both weight classes of the CTC group, its percentage of total IRI among large amberjack was twice that found among the small amberjack (Figures 2 and 4). Additionally, Teuthoidea and Myctophidae appeared to be major food items in both weight classes of the CTC group, but were not present as such in either of the weight classes of the non- CTC group.

Classification of prey into ecological habitats revealed that small CTC amberjack fed more on bottom prey and midwater prey was secondary in importance (Table 5, Figure 6). The reverse situation was true among the small non-CTC amberjack (Figure 7, Table 6).

Large amberjack of both groups showed an increase in water column-associated prey and a decrease in bottom prey (Figures 8 and 9, Tables 7 and 8) compared with small amberjack (Figures 6 and 7, Tables 5 and 6), particularly within the CTC group. The small CTC amberjack were unique in having higher contributions of bottom prey than midwater prey in their diet.

The parasites found most frequently among the stomach contents of CTC and non-CTC amberjack were nematodes and trematodes. The nematode-trematode ratio ranged from 2 to 3:1 in both weight classes of the CTC and non-CTC groups.

The diet of non-CTC amberjack was compared between fish from the NWHI and the LMHI. For small amberjack in both areas, fish were the predominant class taxon and minor contributions were made by crustaceans and cephalopods (Tables 2 and 9). In the NWHI, Octopoda dominated among lower taxa (IRI = 572) followed by *Decapterus* spp. (IRI = 180), Natantia (IRI = 159), and Ammodytidae (IRI = 109) (Figure 10, Table 9). In contrast, the LMHI samples exhibited a great predominance of *Decapterus* spp. followed by Natantia and *S. maunaloae* (Figure 3, Table 2).

The most important class taxon among large amberjack in both areas was fish and less important were crustaceans and cephalopods (Tables 4 and 10). In the NWHI, *D. tabl* (IRI = 660) was the highest ranked lower taxon followed by Teuthoidea (IRI = 375), *Decapterus* spp. (IRI = 235), Balistidae (IRI = 167), fish (IRI = 164), and Tetraodontidae (IRI = 141) (Figure 11, Table 10). This contrasts with the high predominance of *Decapterus* spp. followed by *A. thazard* in the LMHI (Figure 5, Table 4).

In the NWHI Octopoda predominated among the small size class whereas *D. tabl* dominated in the large class, while in the LMHI, *Decapterus* spp. dominated among both weight classes.

TABLE 5. PREY ITEMS OF SMALL CTC AMBERJACK FROM THE LOWER MAIN HAWAIIAN ISLANDS (N = 84) GROUPED BY ECOLOGICAL HABITAT (BOTTOM, MIDWATER, AND BOTH) SHOWING THE DIETARY CONTRIBUTION (IRI) OF EACH HABITAT

Primarily bottom prey

Ammodytidae
Anguilliformes
Anthias sp.
Antigonia steindachneri
Balistidae
Bleekeria gilli
Chaetodontidae
Congridae
Dactylopteridae
Embolichthys sp.
Emmelichthyidae
Gobiidae
Grammatonotus laysanus
Labridae
Lutjanidae
Munida sp.
Octopoda
Paguridae
Penaeidea
Percophididae
Pleuronectiformes
Pomacentridae
Pontinus macrocephala
Portunidae
Priacanthidae
Pristipomoides sp.
Reptantia
Scorpaenidae
Serranidae
Symphysanodon maunaloae
Symphysanodon typus
Synodontidae
Xanthichthys mento

%N	%F	%V	IRI
36.6	61.9	49.4	5,323

Primarily midwater prey

Auxis thazard
Decapterus spp.
Engraulidae
Myctophidae
Teuthoidea

%N	%F	%V	IRI
28.4	44.0	40.5	3,032

Prey primarily associated with both habitats

Caridea
Heterocarpus ensifer
Plesionika longirostris
Plesionika sp.
Mullidae
Natantia
Selar crumenophthalmus
Sphyraenidae
Tetraodontidae

%N	%F	%V	IRI
35.1	19.0	10.1	859

Omitted prey

Carangidae
Cephalopods
Crustaceans
Fish

Note: N = total number, F = frequency of occurrence, V = aggregate total volume, IRI = index of relative importance

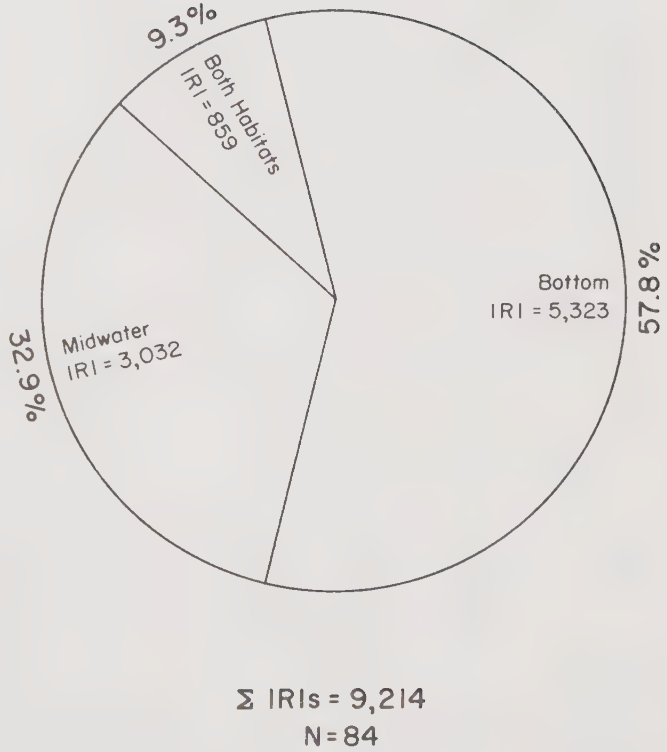

Figure 6. Relative contribution (percent of total IRI) of the three prey habitat types in the diet of small CTC amberjack from the LMHI

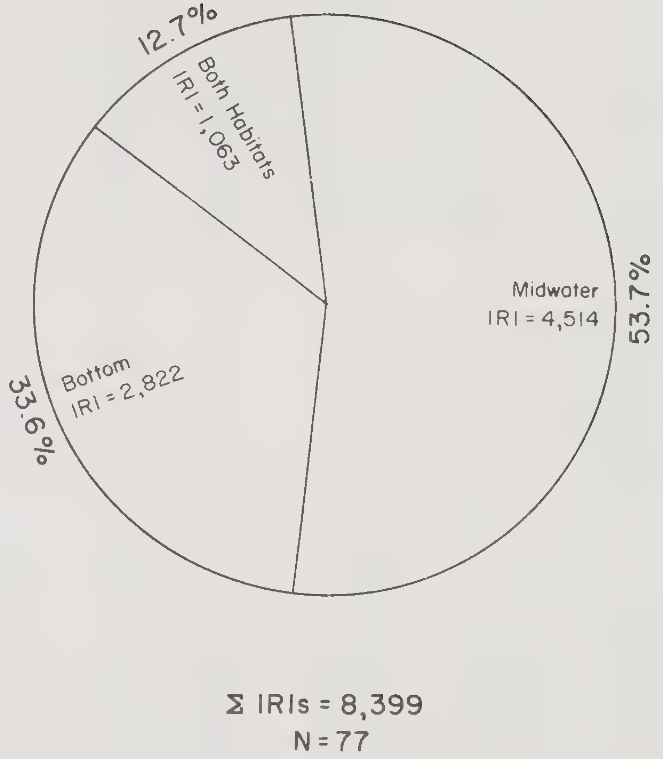

Figure 7. Relative contribution (percent of total IRI) of the three prey habitat types in the diet of small non-CTC amberjack from the LMHI

TABLE 6. PREY ITEMS OF SMALL NON-CTC AMBERJACK FROM THE LOWER MAIN HAWAIIAN ISLANDS (N = 77) GROUPED BY ECOLOGICAL HABITAT (BOTTOM, MIDWATER, AND BOTH) SHOWING THE DIETARY CONTRIBUTION (IRI) OF EACH HABITAT

Primarily bottom prey

Anthias sp.
Bothidae
Caproidae
Emmelichthyidae
Etelis coruscans
Labridae
Lutjanidae
Octopoda
Percophididae
Priacanthidae
Pristipomoides sp.
Reptantia
Scorpaenidae
Scorpaenopsis sp.
Serranidae
Symphysanodon maunaloae
Symphysanodon sp.
Symphysanodon typus
Synodontidae

%N	%F	%V	IRI
39.3	48.0	19.5	2,822

Primarily midwater prey

Decapterus macrosoma
Decapterus spp.
Engraulidae
Myctophidae
Teuthoidea

%N	%F	%V	IRI
15.9	52.0	70.9	4,514

Prey primarily associated with both habitats

Caridea
Heterocarpus ensifer
Mullidae
Natantia
Selar crumenophthalmus
Tetraodontidae

%N	%F	%V	IRI
44.9	19.5	9.6	1,063

Omitted prey

Carangidae
Cephalopods
Crustaceans
Fish

Note: N = total number, F = frequency of occurrence, V = aggregate total volume, IRI = index of relative importance

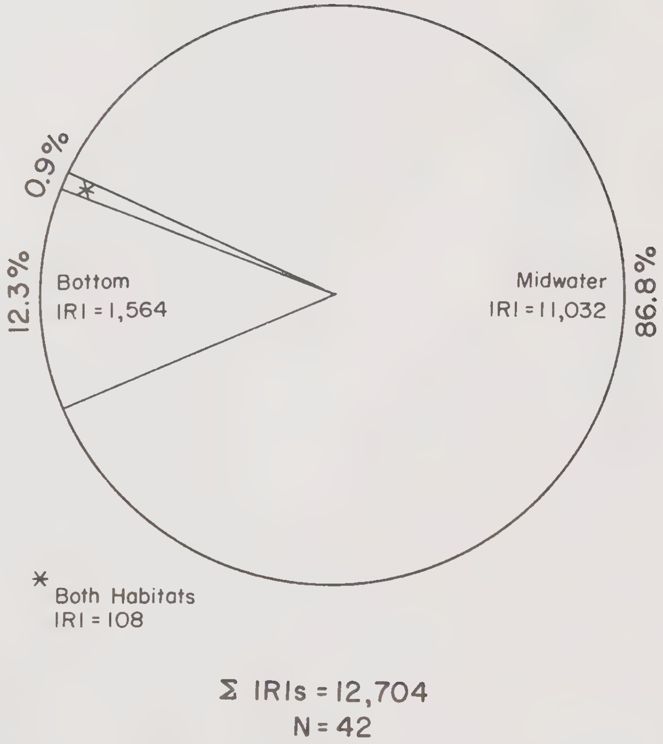

Figure 8. Relative contribution (percent of total IRI) of the three prey habitat types in the diet of large CTC amberjack from the LMHI

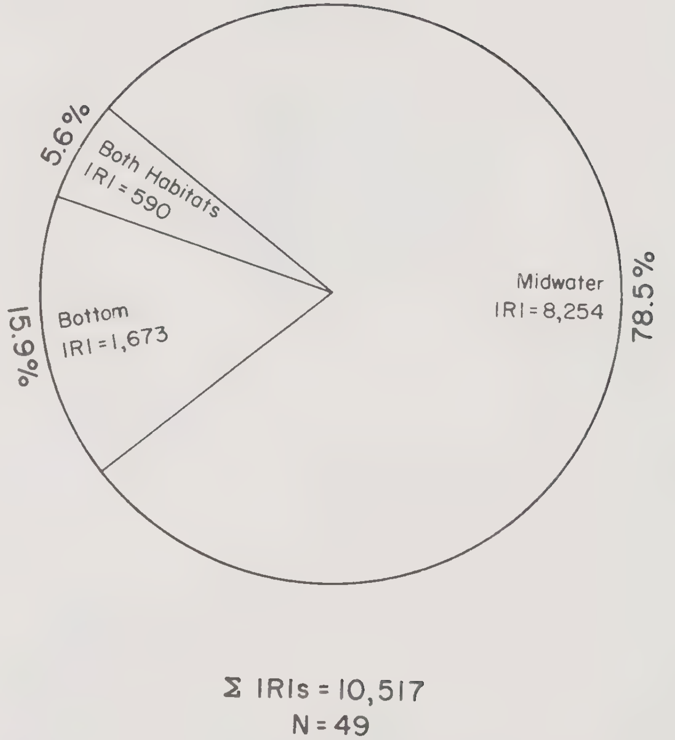

Figure 9. Relative contribution (percent of total IRI) of the three prey habitat types in the diet of large non-CTC amberjack from the LMHI

TABLE 7. PREY ITEMS OF LARGE CTC AMBERJACK FROM THE LOWER MAIN HAWAIIAN ISLANDS (N = 42) GROUPED BY ECOLOGICAL HABITAT (BOTTOM, MIDWATER, AND BOTH) SHOWING THE DIETARY CONTRIBUTION (IRI) OF EACH HABITAT

Primarily bottom prey

- Balistidae
- Bothidae
- Dactylopteridae
- Fistulariidae
- Mullidae
- Octopoda
- Pleuronectiformes
- *Pontinus macrocephala*
- Priacanthidae
- *Pristipomoides sieboldii*
- Synodontidae

%N	%F	%V	IRI
9.9	28.6	44.8	1,564

Primarily midwater prey

- *Ariomma* sp.
- *Auxis rochei*
- *Auxis* sp.
- *Auxis thazard*
- *Decapterus macrosoma*
- *Decapterus* spp.
- Engraulidae
- Gonostomatidae
- Myctophidae
- Scombridae
- Teuthoidea

%N	%F	%V	IRI
84.2	81.0	52.0	11,032

Prey primarily associated with both habitats

- Caridea
- *Heterocarpus ensifer*
- Natantia
- Tetraodontidae

%N	%F	%V	IRI
5.9	11.9	3.2	108

Omitted prey

- Carangidae
- Fish

Note: N = total number, F = frequency of occurrence, V = aggregate total volume, IRI = index of relative importance

TABLE 8. PREY ITEMS OF LARGE NON-CTC AMBERJACK FROM THE LOWER MAIN HAWAIIAN ISLANDS (N = 49) GROUPED BY ECOLOGICAL HABITAT (BOTTOM, MIDWATER, AND BOTH) SHOWING THE DIETARY CONTRIBUTON (IRI) OF EACH HABITAT

Primarily bottom prey

Balistidae
Fistulariidae
Labridae
Lutjanidae
Lutjanus sp.
Moridae
Octopoda
Penaeidea
Polymixiidae
Pristipomoides sieboldii
Pristipomoides sp.
Reptantia
Scorpaenidae
Symphysanodon maunaloae
Symphysanodon typus
Synodontidae
Triglidae

%N	%F	%V	IRI
26.3	34.7	21.9	1,673

Primarily midwater prey

Amphipoda
Auxis sp.
Auxis thazard
Ariomma sp.
Decapterus macrosoma
Decapterus spp.
Myctophidae
Paralepididae
Scombridae
Squilla sp.
Teuthoidea

%N	%F	%V	IRI
43.4	71.4	72.2	8,254

Prey primarily associated with both habitats

Caridea
Heterocarpus ensifer
Natantia
Selar crumenophthalmus
Tetraodontidae

%N	%F	%V	IRI
30.3	16.3	5.9	590

Omitted prey

Carangidae
Cephalopods
Crustaceans
Fish

Note: N = total number, F = frequency of occurrence, V = aggregate total volume, IRI = index of relative importance

TABLE 9. PREY ITEMS OF SMALL NON-CTC AMBERJACK FROM THE NORTHWESTERN HAWAIIAN ISLANDS (N = 92) LISTED IN DECREASING IMPORTANCE BY TAXA. TAXA OF LESSER PREY (THOSE WITH IRI VALUES BELOW 100) ARE LISTED WITH THEIR RESPECTIVE IRI VALUES ONLY.

	%N	%F	%V	IRI
Taxa of prey				
Fishes	60.6	82.6	66.3	10,482
Cephalopods	8.7	25.0	31.1	995
Crustaceans	30.7	13.0	2.6	433
Major lower taxa prey				
Octopoda	4.9	16.3	30.2	572
Decapterus spp.	2.6	10.9	13.9	180
Natantia	27.6	5.4	1.9	159
Ammodytidae	11.2	7.6	3.2	109

Taxa of lesser prey

Serranidae	81	Carangidae (jack)	2
Fish	73	*Scomber japonicus*	2
Teuthoidea	45	Fistulariidae	1
Anthias sp.	44	Mullidae	1
Emmelichthyidae	40	Ostraciontidae	1
Tetraodontidae	40	Penaeidea	1
Priacanthidae	36	Percophididae	1
Embolichthys sp.	25	Acanthuridae	<1
Pseudomonocanthus garretti	18	Argentinidae	<1
		Bleekeria gilli	<1
Symphysanodon maunaloae	17	Bothidae	<1
		Bramidae	<1
Congridae	16	Cephalopods	<1
Decapterus tabl	15	Dactylopteridae	<1
Crustaceans	11	Euphausiacea	<1
Ariomma sp.	6	Exocoetidae	<1
Synodontidae	6	Moridae	<1
Balistidae	4	Nomeidae	<1
Myctophidae	4	Pegasidae	<1
Pleuronectiformes	4	*Psenes* sp.	<1
Symphysanodon typus	4	Reptantia	<1
Anguilliformes	2	Scorpaenidae	<1
Aracana aculeata	2	Triglidae	<1
Caproidae	2	Zeidae	<1

Note: N = total number, F = frequency of occurrence, V = aggregate total volume, IRI = index of relative importance

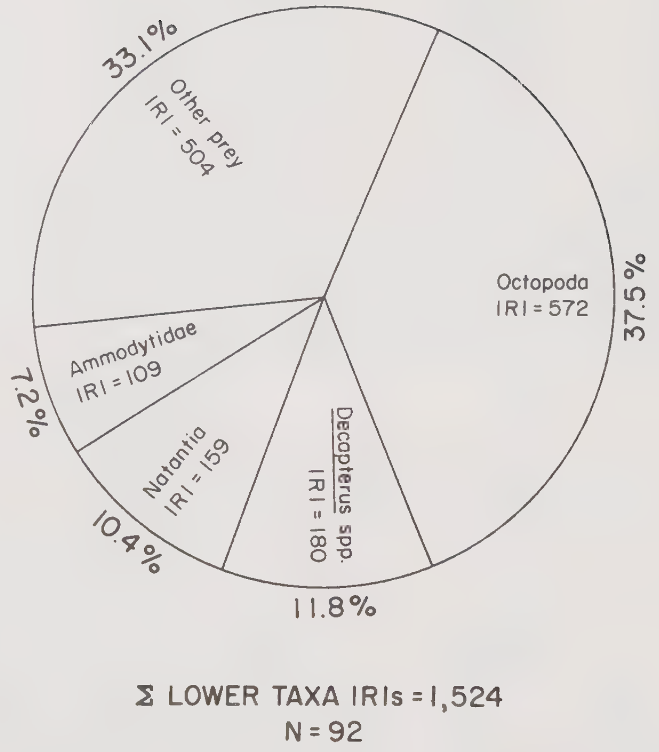

Figure 10. Relative contribution (percent of total IRI) of prey in the diet of small non-CTC amberjack from the NWHI. Taxa of lesser prey are grouped together in the "other prey" category.

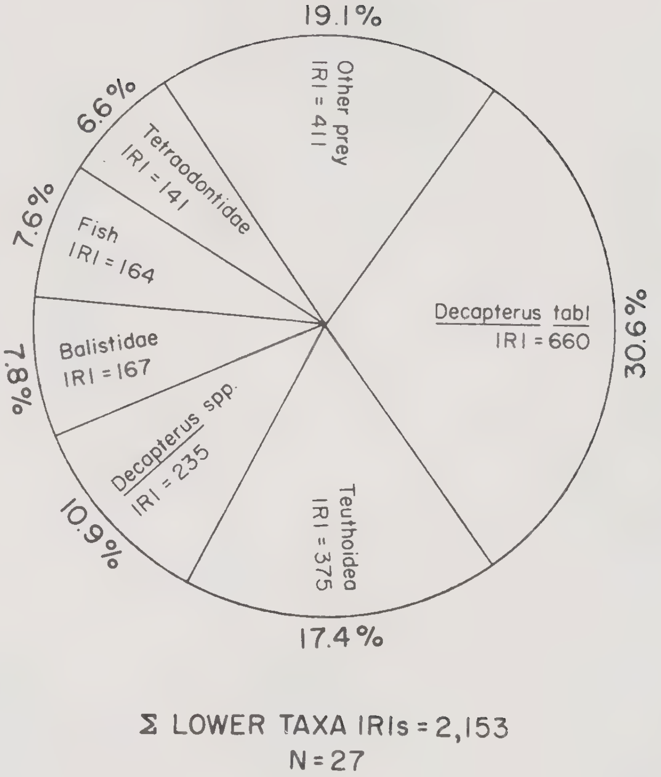

Figure 11. Relative contribution (percent of total IRI) of prey in the diet of large non-CTC amberjack from the NWHI. Taxa of lesser prey are grouped together in the "other prey" category.

TABLE 10. PREY ITEMS OF LARGE NON-CTC AMBERJACK FROM THE NORTHWESTERN HAWAIIAN ISLANDS (N = 27) LISTED IN DECREASING IMPORTANCE BY TAXA. TAXA OF LESSER PREY (THOSE WITH IRI VALUES BELOW 100) ARE LISTED WITH THEIR RESPECTIVE IRI VALUES ONLY.

	%N	%F	%V	IRI
Taxa of prey				
Fishes	58.2	77.8	96.2	12,012
Cephalopods	20.9	33.3	3.1	799
Crustaceans	20.9	18.5	0.7	400
Major lower taxa prey				
Decapterus tabl	9.9	14.8	34.7	660
Teuthoidea	16.5	22.2	0.4	375
Decapterus spp.	5.5	14.8	10.4	235
Balistidae	12.1	7.4	10.5	167
Fish	6.6	22.2	0.8	164
Tetraodontidae	3.3	11.1	9.4	164

Taxa of lesser prey

Pseudomonocanthus garretti	82	*Symphysanodon maunaloae*	8
Octopoda	79	Carangidae	6
Fistulariidae	75	Polymixiidae	6
Crustaceans	64	Priacanthidae	6
Reptantia	37	Anguilliformes	4
Muraenidae	14	Argentinidae	4
Congridae	9	Natantia	4
Mullidae	9	Synodontidae	4

Note: N = total number, F = frequency of occurrence, V = aggregate total volume, IRI = index of relative importance

The results of habitat classification of prey revealed that among small NWHI amberjack, bottom-associated prey was most important (Table 11, Figure 12), whereas for small LMHI amberjack, the water column-associated prey dominated (Figure 7, Table 6). For large NWHI amberjack, bottom prey ranked higher than midwater prey (Figure 13, Table 12). However, the large LMHI amberjack showed a predominance of midwater prey (Figure 9, Table 8).

The dietary change from small to large amberjack in both areas involved an increase of midwater prey and a decrease in bottom prey.

Nematodes and trematodes were the most frequent gut parasites, regardless of weight class and area. The ratio of nematodes to trematodes for the NWHI sample ranged from 3 to 4:1 compared with 2 to 3:1 for the LMHI sample.

TABLE 11. PREY ITEMS OF SMALL NON-CTC AMBERJACK FROM THE NORTHWESTERN HAWAIIAN ISLANDS (N = 85) GROUPED BY ECOLOGICAL HABITAT (BOTTOM, MIDWATER, AND BOTH) SHOWING THE DIETARY CONTRIBUTION (IRI) OF EACH HABITAT

Primarily bottom prey

- Acanthuridae
- Ammodytidae
- Anguilliformes
- *Anthias* sp.
- *Aracana aculeata*
- Balistidae
- *Bleekeria gilli*
- Bothidae
- Caproidae
- Carangidae
- Congridae
- Dactylopteridae
- *Embolichthys* sp.
- Emmelichthyidae
- Fistulariidae
- Moridae
- Octopoda
- Ostraciontidae
- Pegasidae
- Penaeidea
- Percophididae
- Pleuronectiformes
- Priacanthidae
- *Pseudomonocanthus garretti*
- Reptantia
- *Scomber japonicus*
- Scorpaenidae
- Serranidae
- *Symphysanodon maunaloae*
- *Symphysanodon typus*
- Synodontidae
- Triglidae

%N	%F	%V	IRI
53.6	74.1	71.1	9,240

Primarily midwater prey

- Argentinidae
- *Ariomma* sp.
- Bramidae
- *Decapterus* spp.
- *Decapterus tabl*
- Exocoetidae
- Myctophidae
- Nomeidae
- *Psenes* sp.
- Teuthoidea

%N	%F	%V	IRI
9.3	36.5	23.2	1,186

Prey primarily associated with both habitats

- Euphausiacea
- Mullidae
- Natantia
- Tetraodontidae
- Zeidae

%N	%F	%V	IRI
37.1	14.1	5.7	603

Omitted prey

- Cephalopods
- Crustaceans
- Fish

Note: N = total number, F = frequency of occurrence, V = aggregate total volume, IRI = index of relative importance

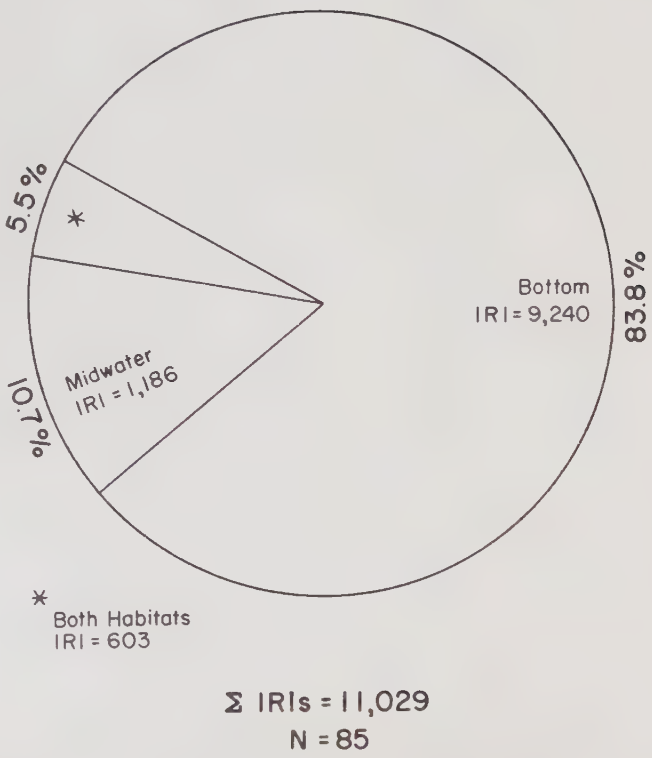

Figure 12. Relative contribution (percent of total IRI) of the three prey habitat types in the diet of small non-CTC amberjack from the NWHI

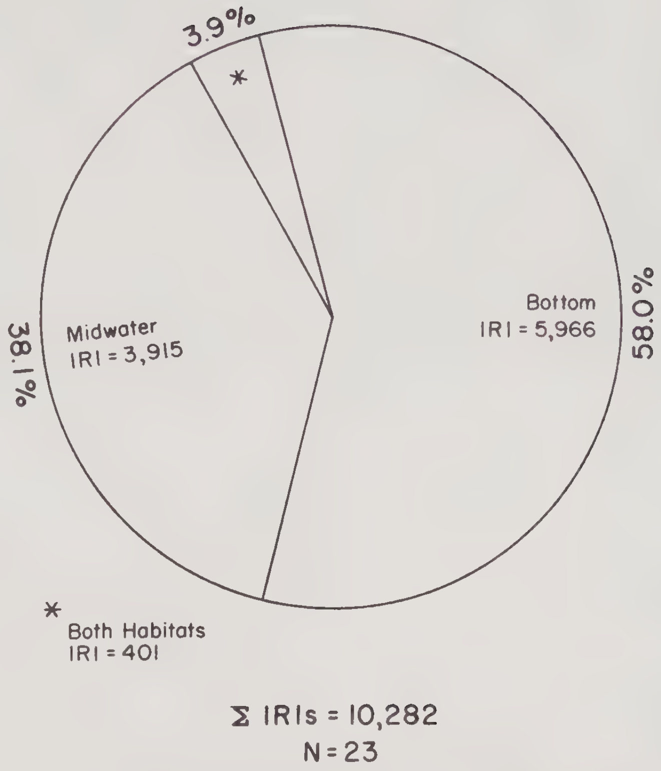

Figure 13. Relative contribution (percent of total IRI) of the three prey habitat types in the diet of large non-CTC amberjack from the NWHI

TABLE 12. PREY ITEMS OF LARGE NON-CTC AMBERJACK FROM THE NORTHWESTERN HAWAIIAN ISLANDS (N = 23) GROUPED BY ECOLOGICAL HABITAT (BOTTOM, MIDWATER, AND BOTH) SHOWING THE DIETARY CONTRIBUTION (IRI) OF EACH HABITAT

Primarily bottom prey

- Anguilliformes
- Balistidae
- Congridae
- Fistulariidae
- Muraenidae
- Octopoda
- Polymixiidae
- Priacanthidae
- *Pseudomonocanthus garretti*
- Reptantia
- *Symphysanodon maunaloae*
- Synodontidae

%N	%F	%V	IRI
47.8	65.2	43.7	5,966

Primarily midwater prey

- Argentinidae
- *Decapterus* spp.
- *Decapterus tabl*
- Teuthoidea

%N	%F	%V	IRI
43.5	43.5	46.5	3,915

Prey primarily associated with both habitats

- Mullidae
- Natantia
- Tetraodontidae

%N	%F	%V	IRI
8.7	21.7	9.8	401

Omitted prey

- Carangidae
- Crustaceans
- Fish

Note: N = total number, F = frequency of occurrence, V = aggregate total volume, IRI = index of relative importance

DISCUSSION

Decapterus spp. were the most important lower prey taxon in the diet of LMHI amberjack, regardless of their toxicity or size. *Decapterus* spp. were also the most important component among the midwater prey which dominated in the non-CTC and large CTC amberjack. Among small CTC amberjack, however, *Decapterus* spp. were less predominant and this was reflected in the higher contribution of bottom prey as opposed to midwater prey. Therefore, dietary differences between the small CTC amberjack and the other three groups are primarily reflected in the smaller contribution of *Decapterus* spp. in the former group. To help understand the dietary differences observed thus far in relation to whether

Decapterus spp. might be involved in the transmission of ciguatoxin, the following pertinent information is summarized.

The genus *Decapterus* is represented by four species within the Hawaiian Archipelago. *Decapterus macarellus* is the most abundant species in the LMHI but in the NWHI their abundance is unknown. In this paper this species is called *Decapterus* spp. because *D. macarellus* and *D. muroadsi* (an infrequent conspecific), are not readily distinguishable. The other two species, *D. macrosoma* and *D. tabl*, are easily distinguishable from each other as well as from *Decapterus* spp.

A life history study by Yamaguchi (1953) characterized *D. macarellus* as usually inhabiting the middle and upper layers of the neritic zone, although at times being found in shallow water and far out at sea. Yamaguchi concluded that *D. macarellus* fed on zooplankton, primarily crustaceans. Dietary studies on other members of the genus, including *D. tabl*, showed them to be primarily planktivorous (Tiews et al., 1970). This feeding mode among members of *Decapterus* indicates little interaction with benthic fauna. Assuming that ciguatoxin has a benthic origin in the LMHI, similar to what Yasumoto et al. (1977a, 1977b) found in French Polynesia, *Decapterus* appears to be an unlikely intermediary for ciguatoxin transmission through the food chain. Additionally, *Decapterus* is a popular food fish in Hawaii, yet Kubota (1981) found no instances of it being implicated among reported ciguatera poisoning cases from 1900 to December 1980. From this background information, several hypotheses have been developed to explain the dietary patterns found among the four groups investigated in the LMHI.

For amberjack, a temporal and spatial change of available prey would prevail when *Decapterus* is absent or scarce. In this situation the most abundant prey would then be bottom forms because *Decapterus* appears to be the only abundant midwater prey in the diet. If this switch to feeding on bottom prey coincided with ciguatoxicity among the local reef fauna, the link in the transmission of ciguatoxin would be completed. This chain of events would explain the lower *Decapterus*, higher bottom prey tendencies that occur in the small CTC amberjack. It is also assumed that large CTC and non-CTC amberjack possess increased mobility and speed, thus enhancing their ability to capture and consume larger and faster midwater prey. This is evident by the large amounts of *Decapterus* and the occurrence of *Auxis* in their diet. Hence, large amberjack are probably less apt to feed on bottom prey if midwater prey are readily available. Kimura et al. (1981) found that large amberjack had the same incidence of ciguatoxicity as small ones for the LMHI and NWHI areas combined. Thus ciguatoxin appears more likely to be transmitted to small rather than large amberjack. Ciguatoxicity in large amberjack is likely attributable to the retention of ciguatoxin from an earlier exposure. Although ciguatoxin retention in kahala has not been investigated, Banner et al. (1966) did conduct such a study on the reef carnivore, *Lutjanus bohar*, from Christmas

Island. Results indicated that no statistically detectable losses in toxicity occurred among a group of _L_. _bohar_ held in captivity at Coconut Island, Oahu, Hawaii for up to 30 months. Banner et al. did qualify their results, however, by suggesting that the toxicity level in some ciguatoxic fish may gradually diminish over time.

These hypotheses, however, appear to be contradicted by the NWHI amberjack. The diet of small non-CTC amberjack in the NWHI contains more bottom prey than that of the small CTC amberjack in the LMHI. With greater feeding of amberjack on bottom prey, the incidence of ciguatoxicity among amberjack in the NWHI would be expected to be higher than the toxicity rate determined for the LMHI fish. However, Polovina and Ito (1981) found no apparent relationship between incidence of toxicity and area. It therefore appears plausible, as shown by Yasumoto et al. (1979) in the overall higher population counts of _G_. _toxicus_ at Gambier Islands compared with Tahiti, that the NWHI offer less suitable conditions for ciguatoxin outbreaks than the LMHI. If this situation is true, then the increased utilization of bottom prey by NWHI amberjack would not necessarily cause a greater incidence of ciguatoxicity when compared with the LMHI. Still unaccounted for is the reason for the increase in bottom prey in both weight groups in the NWHI, when _Decapterus_ is known to occur there, perhaps in great abundance. The high occurrence of Octopoda in the diet of the small NWHI amberjack is the only instance of a lower prey taxon exceeding _Decapterus_ spp. and _D_. _tabl_ in percentage of total IRI. By comparison, Octopoda in all four groups in the LMHI is consistently negligible. It thus appears plausible that sufficient readily available bottom prey exists within the NWHI such that midwater prey, namely _Decapterus_, are fed upon less often by the small amberjack. Even so, the trend toward increased midwater prey in the diet as the amberjack grows larger in the LMHI is also evident in the NWHI, although to a lesser degree. This trend apparently indicates that the large NWHI amberjack are increasingly capable of consuming the swifter and frequently larger midwater prey, a situation more strongly indicated by their weight class counterparts in the LMHI.

CONCLUSIONS

Data presented in this report support the hypothesis that small amberjack in the LMHI are more susceptible to becoming ciguatoxic when feeding preference shifts away from _Decapterus_ to bottom prey. Since large amberjack feed more on _Decapterus_, the occurrence of large CTC amberjack is mainly attributed to ciguatoxin's long retention time. The data also suggest that a more readily available bottom prey fauna exists in the NWHI and that conditions for CTC outbreaks are less than optimal there compared with the LMHI. Tests of these hypotheses should address the following: determination of ciguatoxicity in _Decapterus_ and bottom prey species over time and area; diet of CTC amberjack from the NWHI; retention time of ciguatoxin in amberjack; confirmation of a solely benthic mode of ciguatera origin and, if so, the determination of population abundance of the ciguatoxin-producing agent in the NWHI and LMHI.

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SEAMOUNT FISHERY RESOURCES WITHIN THE SOUTHERN EMPEROR-NORTHERN HAWAIIAN RIDGE AREA

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ABSTRACT

The summits of the seamounts comprising the southern Emperor Seamount Chain and northern Hawaiian Ridge (Koko-Hancock Seamounts) lie at depths of 250 to 400 m; Russian data indicate that the topography produces much surface current meandering and upwelling in the region. In 1967, Soviet trawl fishermen discovered vast quantities of pelagic armorhead, *Pentaceros richardsoni*, and to a lesser extent alfonsin, *Beryx splendens*, closely associated with summits of these seamounts. Two years later, Japanese trawlers entered the fishery. They achieved their highest annual catch per unit of effort in 1972 with a sharp decline after 1976. With the advent of the 200-mile U.S. fishery conservation zone, the Hancock Seamounts came under U.S. jurisdiction. Comparison of the U.S. foreign observer data obtained on Japanese trawlers in 1978-82 with earlier Japanese data show trawl catches on Hancock have generally been declining since the high catch of 1972. Seamounts of the Hawaiian Ridge located south of Hancock and east of 180° longitude differ in having shallower summits, higher summit water temperatures, and fish faunas dominated by subtropical reef and snapper-grouper species. Meristic and electrophoretic work on pelagic armorhead indicates the existence of one stock inhabiting the range of seamounts between Koko and Hancock. Morphological variation among pelagic armorhead is little understood.

alfonsin
pelagic armorhead
seamounts

INTRODUCTION

The islands, banks, reefs, and seamounts of the Hawaiian Ridge extend northwesterly from the island of Hawaii some 3,500 km to Colahan Seamount. To the northwest of Colahan the Emperor Seamounts extend from the Milwaukee Seamount Group northward 2,300 km to Meiji Seamount (Jackson et al., 1980). The Emperor-Hawaiian Ridge area is composed of at least 107 identifiable volcanoes from which all the associated topographical features originate. These volcanoes are thought to have been produced by the northward movement of the Pacific plate over a "hot spot" with the bend at the junction of the Emperor-Hawaiian Ridge area caused by a shifting of the plate to the northwest. Results from a variety of dating techniques on samples obtained from sites throughout the Emperor-Hawaiian Ridge area show a pattern of increasing age with distance from the island of Hawaii (Dalrymple et al., 1981). This indicates that the seamounts are among the oldest of topographic features within the Emperor-Hawaiian Ridge area. The seamounts discussed in this review are Koko, Yuryaku, and Kammu of the southern Emperor Seamounts Chain and Colahan, C-H, NW Hancock, SE Hancock, Ladd, Nero, and unnamed seamounts 8 to 11 of the northern Hawaiian Ridge. All are situated within an area bounded by lat. 26° to 36°N and long. 174°W to 171°E (Figure 1). A seamount is defined as a more-or-less isolated elevation of the sea floor appearing circular or elliptical in cross-section, with a minimum relief of 1 km, comparatively steep slopes, and a relatively small summit area. Most, if not all, seamounts are volcanic in origin (Menard, 1964).

The seamounts of the southern Emperor-northern Hawaiian Ridge area from Koko to Hancock Seamounts (hereafter designated SE-NHR), lie within the mean flow of the North Pacific Current. Results of Soviet investigations in this region indicate a substantial perturbance in the surface current field, apparently produced by the seamounts (Borets, 1980). Fedosova (1974) reported the existence of cyclonic and anticyclonic eddies over the SE-NHR seamounts. These eddies fluctuated seasonally in location and dimension, but apparently persisted throughout the year.

The sea-surface temperature (SST) annually ranges from 15 to 26°C at Koko Seamount, 18° to 27°C near the Hancock Seamounts, and 22° to 29°C to the south in the vicinity of seamounts 8 and 9. Maximum SST usually occurs during August-September and the temperatures are lowest in February-March (Eber et al., 1968). Unfortunately, temperature data for the seamount summits are scarce, and comparisons are complicated by the wide range in summit elevations. Available data indicate an annual range in summit temperatures of 8° to 15°C among the more northerly seamounts (summit depths of 250 to 400 m) from Yuryaku to SE Hancock. The southern seamounts, from Ladd to seamount 8, have shallower summit depths of 50 to 200 m and temperatures of 14° to 24°C (Japan Marine Fishery Resource Research Center, 1973; Japan Fisheries Agency, 1974; Gooding, 1980).

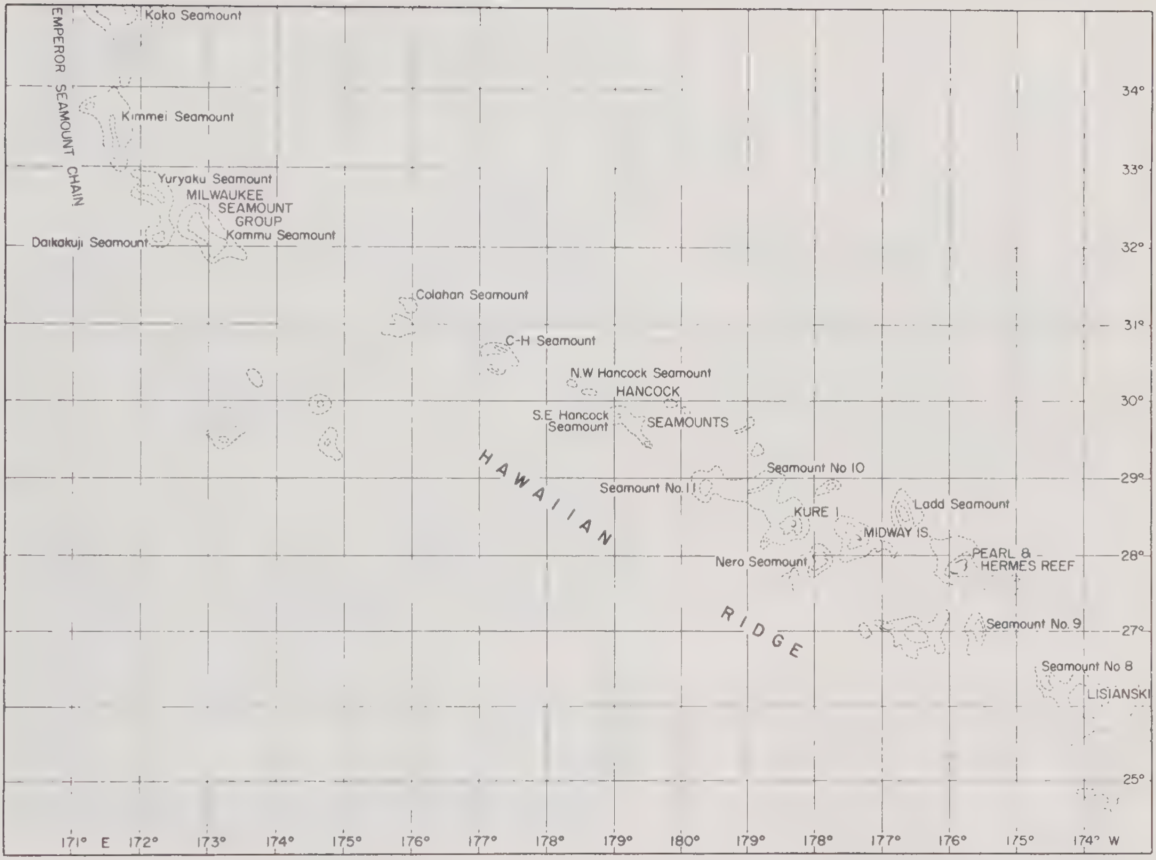

EMPEROR SEAMOUNT CHAIN
Koko Seamount
Kimmei Seamount
Yuryaku Seamount
MILWAUKEE SEAMOUNT GROUP
Daikakuji Seamount
Kammu Seamount
Colahan Seamount
C-H Seamount
N.W Hancock Seamount
HANCOCK SEAMOUNTS
S.E Hancock Seamount
HAWAIIAN RIDGE
Seamount No 10
Seamount No.11
Ladd Seamount
KURE I.
MIDWAY IS.
PEARL & HERMES REEF
Nero Seamount
Seamount No. 9
Seamount No 8
LISIANSKI
34°
33°
32°
31°
30°
29°
28°
27°
25°
171° E
172°
173°
174°
175°
176°
177°
178°
179°
180°
179°
178°
177°
176°
175°
174° W

Figure 1. The southern Emperor-northern Hawaiian Ridge seamounts

Besides fluctuations in the current field and water temperature, seasonal changes in plankton biomass over the seamounts have been observed in the area between lat. 27° and 37°N, long. 170°E and 178°W. Soviet investigators found areas of highest plankton biomass in the spring. These areas were displaced downcurrent of upwelling zones in the winter-spring period, whereas in spring-summer they were found near eddies. The winter-spring conditions were explained relative to the intensification of the North Pacific Current and the directional coincidence of prevailing winds, whereas during spring-summer there was a weakening of this current (Fedosova, 1974). Pontekorvo (1974) suggested that zones of upwelling are produced on opposite sides of a seamount. These zones are roughly aligned with the prevailing current and intensified during the winter. Bezrukov and Natarov (1976) attributed the formation of high biological productivity over the SE-NHR seamounts to a favorable abiotic regime produced by the intense vertical water circulation.

SEAMOUNT TRAWL FISHERY -- PAST AND PRESENT

The discovery of a bottom trawl fishery resource on the SE-NHR seamounts was made by a Soviet commercial trawler in November 1967. The resource consisted primarily of pelagic armorhead, *Pentaceros richardsoni*, and alfonsin, *Beryx splendens* (Figures 2 and 3). Shortly thereafter, a Soviet trawl fishery began on the SE-NHR seamounts. From December 1969 through July 1970, Soviet trawlers harvested approximately 133,400 metric tons (MT) of pelagic armorhead from the seamounts (Sakiura, 1972). This is the only catch data available for the Soviet trawl fleet although Soviet trawlers have probably continued to fish the seamounts to the present. In 1968-69, two Soviet research cruises surveyed an area from lat. 21° to 36°N, and long. 160°E to 165°W. Seamounts surveyed were Koko, Milwaukee (consisting of Kammu, Yuryaku, and Daikakuji Seamounts), Hancock (refers to NW and SE Hancock Seamounts), and two unidentified seamounts. Pelagic armorhead was the principal species caught on each seamount. Total catch of alfonsin ranged from 5 to 30 percent at Koko and accounted for 25 percent at Milwaukee. The catch of alfonsin on the other seamounts was not given. Catches of pelagic armorhead at each seamount were found to vary diurnally. Catches would generally increase after 1800 hours and peak just before sunrise (Sakiura, 1972).

The Japanese seamount trawl fishery began in August 1969. An initial 2-year exploratory phase defined suitable trawl grounds and developed markets for the catch. Unlike the Soviets, the Japanese have made available their trawl catch and effort data, by seamount, for pelagic armorhead and alfonsin caught during 1969-81 (Takahashi and Sasaki, 1977; Sasaki, unpublished data). These data cover trawling on the following seamounts: Koko, Milwaukee, Colahan, C-H, Hancock, and others.

Figure 4 shows the annual effort (in trawl hours) at each of the seamounts during 1969-81. During the exploratory phase Milwaukee was surveyed intensively, whereas during 1972-73 effort was more equitably partitioned among all the seamounts. Effort during the following years (1974-81) was concentrated at Koko and Milwaukee.

The annual catch of pelagic armorhead is shown in Figure 5 for 1969-81. The annual catches fluctuated widely at Milwaukee during 1969-77, whereas they fluctuated less at Koko, Colahan, and Hancock. The fluctuations in catch at Koko and Milwaukee during 1969-71 and 1974-76 appear to coincide with fluctuations in effort. Outside of these fluctuations, the catch record shows two remarkable events. First was the high annual catches at Colahan in 1972 and Hancock in 1973 with a decline and modest increase in effort, respectively. Also, the 1972 catch at Milwaukee showed a large increase compared with the 1971 catch in spite of a decrease in effort. The second event was the plummeting of catches starting in 1977 at Koko and Milwaukee despite increased effort and a subsequent depression in catches at all seamounts through 1981, regardless of changes in effort.

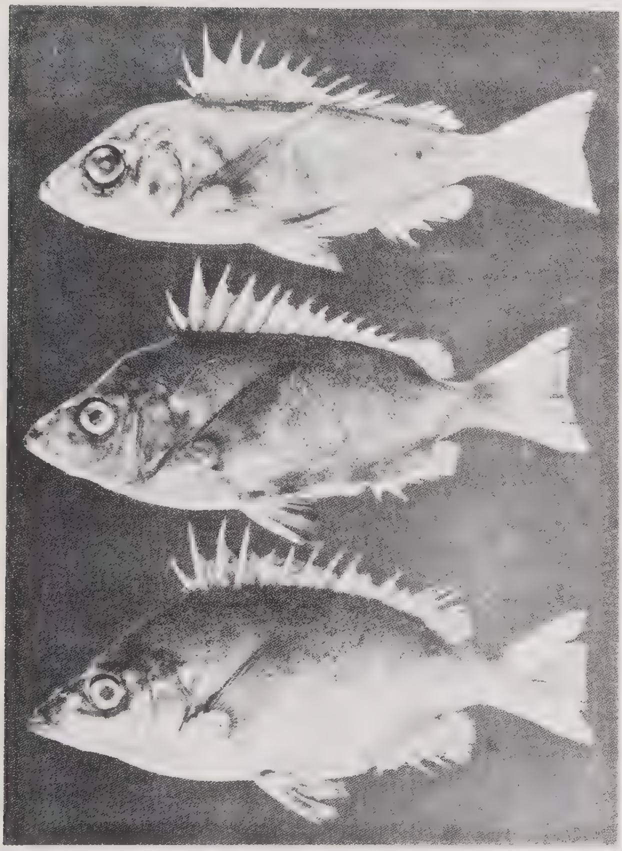
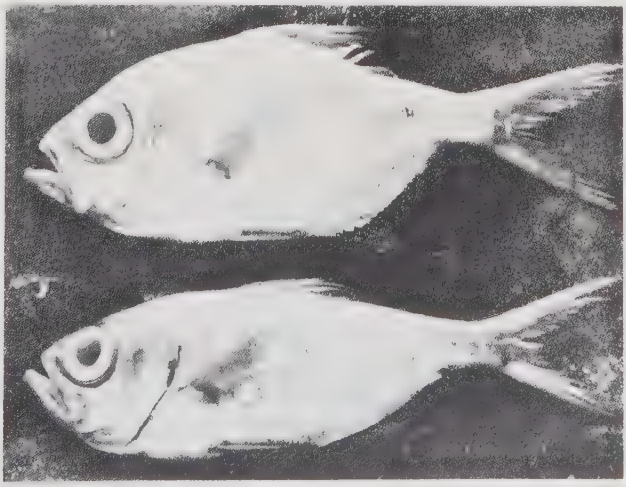


Figure 2. Morphological variation in specimens of pelagic armorhead, *Pentaceros richardsoni*. Upper specimen represents the lean type, middle specimen the intermediate type, and lower specimen the fat type.

Figure 3. Specimens of alfonsin, genus Beryx. Upper specimen is *B. decadactylus* and the lower specimen, *B. splendens*.



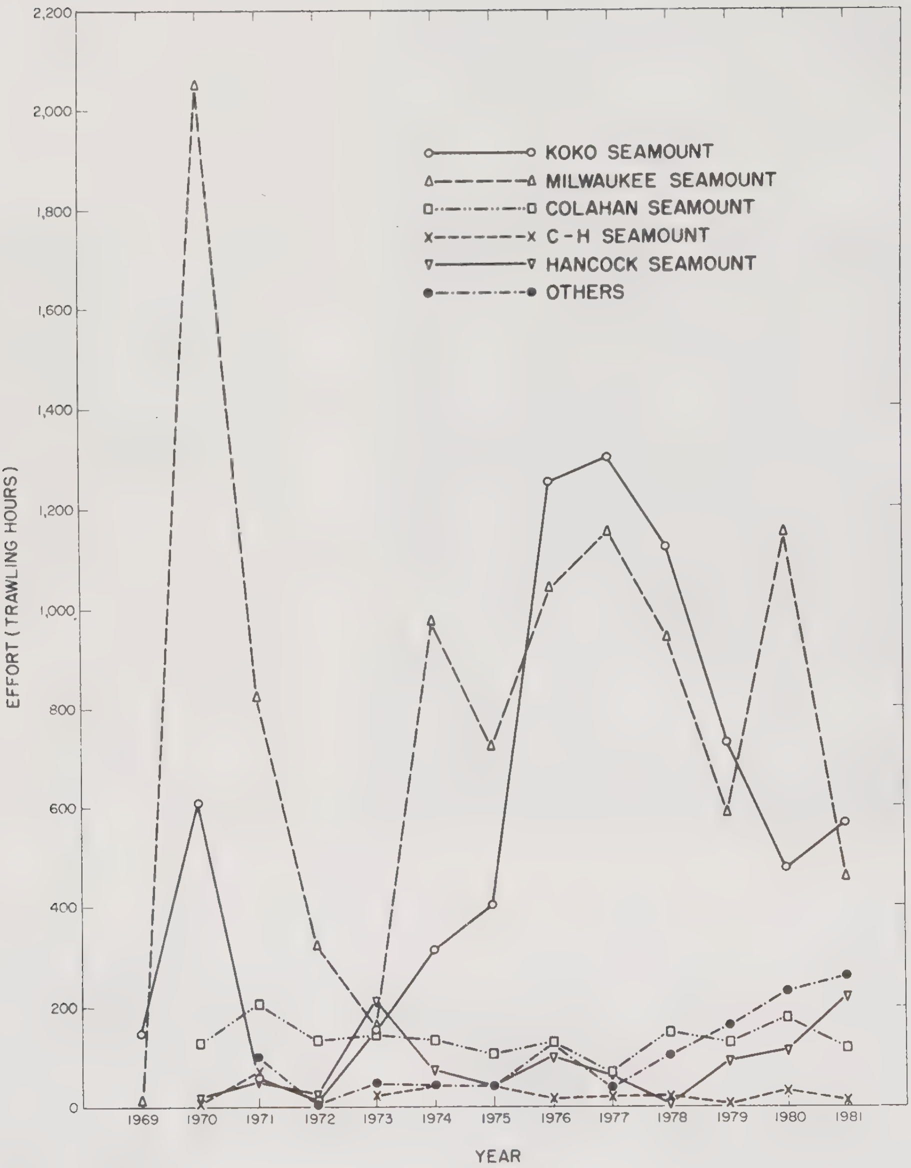


Figure 4. Yearly effort of Japanese trawl fishery for pelagic armorhead and alfonsin at six seamounts within the Emperor-Hawaiian Ridge

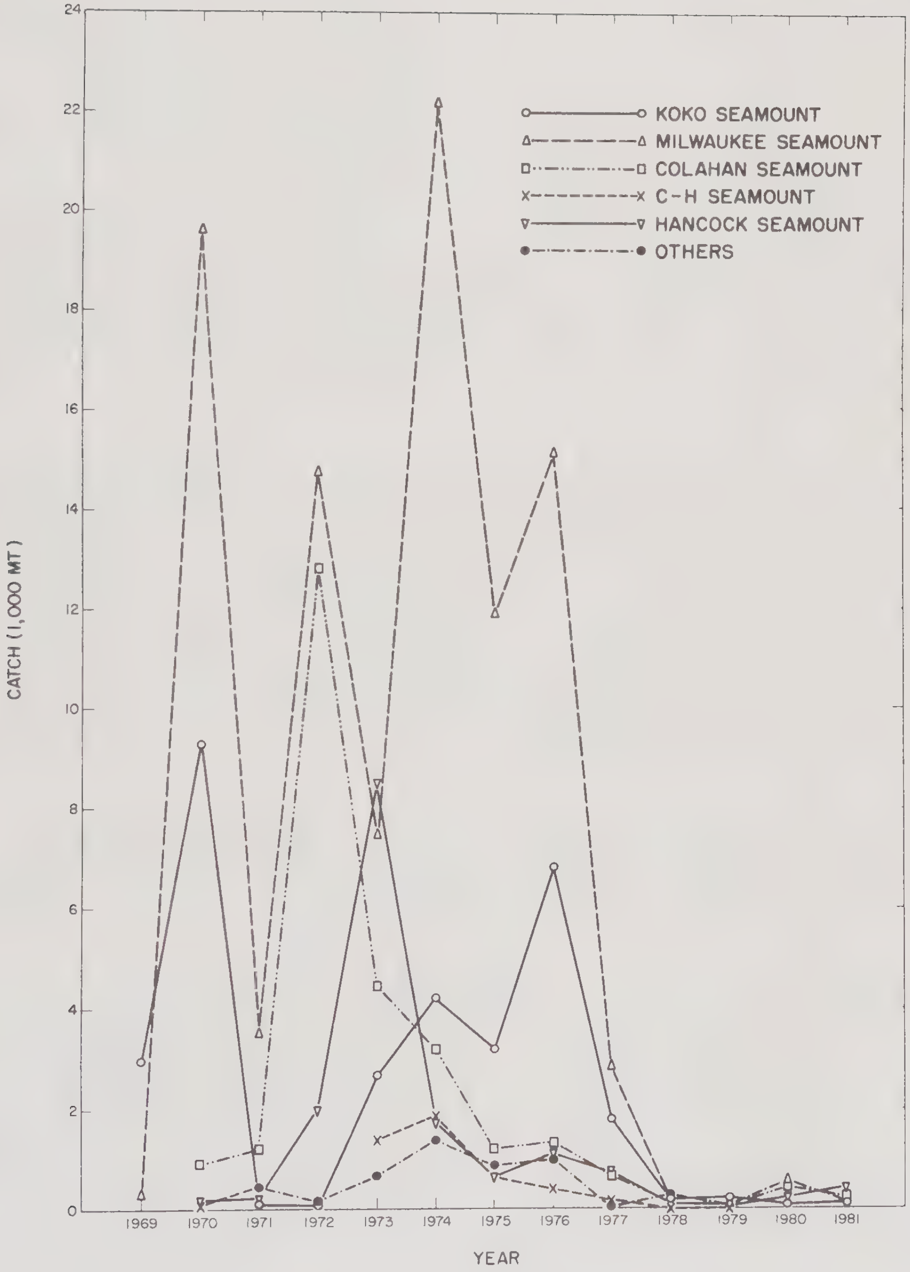


Figure 5. Yearly catch of pelagic armorhead taken by Japanese trawlers at six seamounts within the Emperor-Hawaiian Ridge

The annual Japanese catch per unit effort (CPUE) of pelagic armorhead during 1969-81 is shown in Figure 6. The depressed CPUE during 1969-71 is probably indicative of the exploratory nature of the fishery during this time. The CPUE for all seamounts rose during 1972-73, declined at most seamounts until 1978, and thereafter, remained at a low level through 1981. The general decline reflects the decline in catch over each seamount with the exception of Hancock in 1978 and C-H in 1981. The increased CPUE at Hancock in 1978 resulted from a 178-MT catch during 6 trawling hours in May. A 51-MT catch during 5 trawling hours in January and a 99-MT catch in 7 hours in February accounted for the increase at C-H in 1981. Also the peak CPUE at Hancock in 1972 resulted from a 1,870-MT catch in 24 trawling hours during July. All these CPUEs appear to represent fortuitous increases in pelagic armorhead availability over very short periods of time.

Figure 7 shows a plot of annual catch, effort, and CPUE of pelagic armorhead for all seamounts combined during 1969-81. Although CPUE steadily declined throughout 1973-79, catches were fairly steady during 1972-76 even if more effort was expended during 1974-76 than during the previous 2 years. Although only 5.7 percent (1,236 hours) of the total effort (21,625 hours throughout 1969-81) over all the seamounts was expended during 1972-73, the catch amounted to 29.8 percent (54,927 MT) of a total 184,109 MT harvested from all seamounts during 1969-81. In contrast, the total catch during 1977-81 was only 5.8 percent (10,679 MT) despite the fact that 48.5 percent (10,494 hours) of the total effort was expended.

The highest total catch of pelagic armorhead during 1969-81 occurred at Milwaukee (Figure 8). Milwaukee contributed 53.6 percent toward the total catch and also received the greatest effort (48.0 percent). Hancock contributed 8.7 percent toward the total catch with 4.7 percent of the total effort.

The second species of importance in the Japanese trawl fishery was alfonsin. The annual catches at each seamount, shown in Figure 9, were either small or incompletely reported during 1969-75. Since armorhead is the primary target species of the trawl fishery, catches of alfonsin, although important, are incidental. Apparently no alfonsin catch data were collected and/or published for 1974-75. From 1976 to 1981, all seamounts showed an overall catch increase with the exception of Hancock. Figure 10 also shows a similar trend in CPUE with the exception again at Hancock. These increases in alfonsin catch and CPUE closely coincide with the sharp decreases and sustained depression in catch and CPUE of pelagic armorhead.

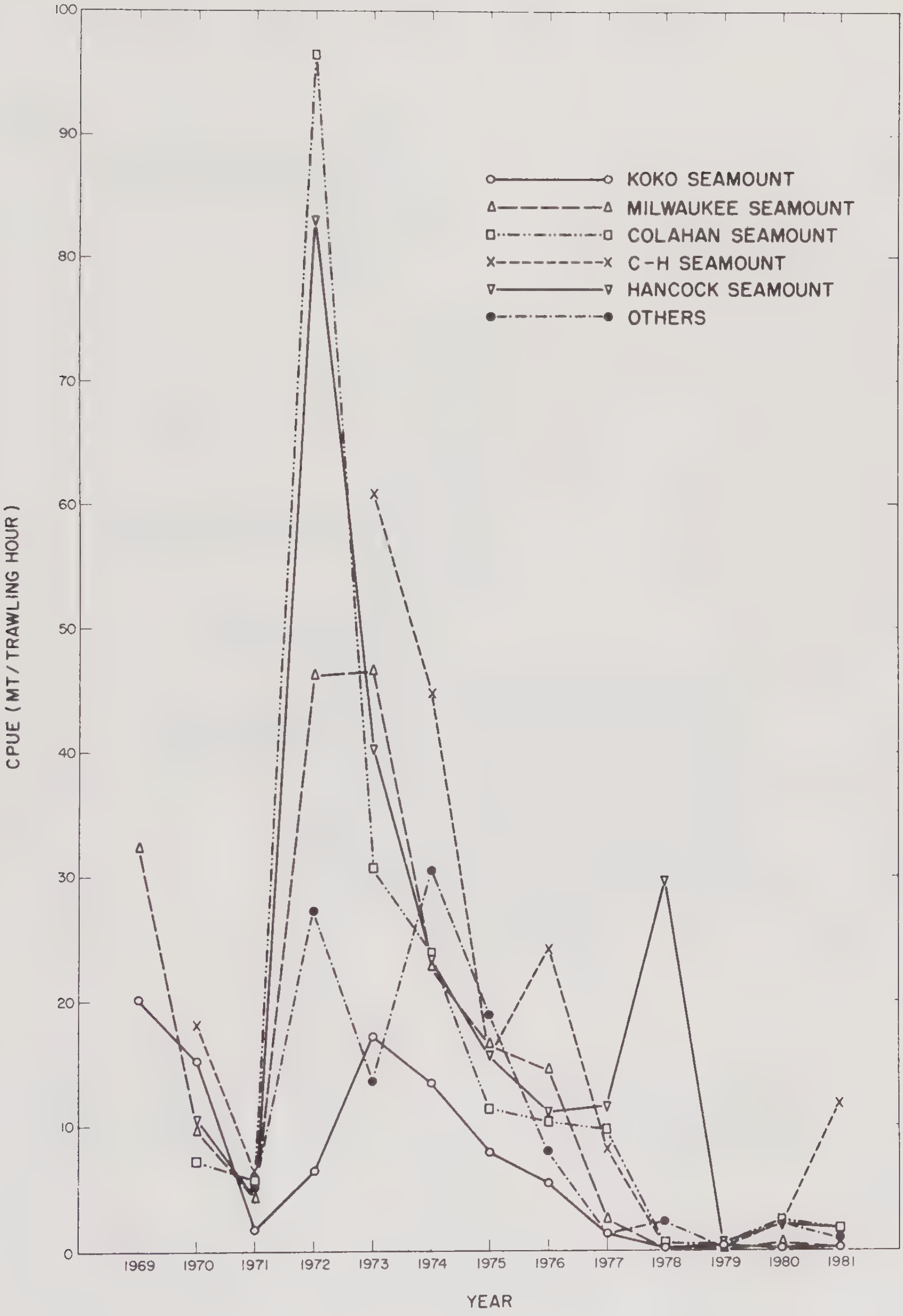


Figure 6. Yearly catch per unit effort of pelagic armorhead taken by Japanese trawlers at six seamounts within the Emperor-Hawaiian Ridge

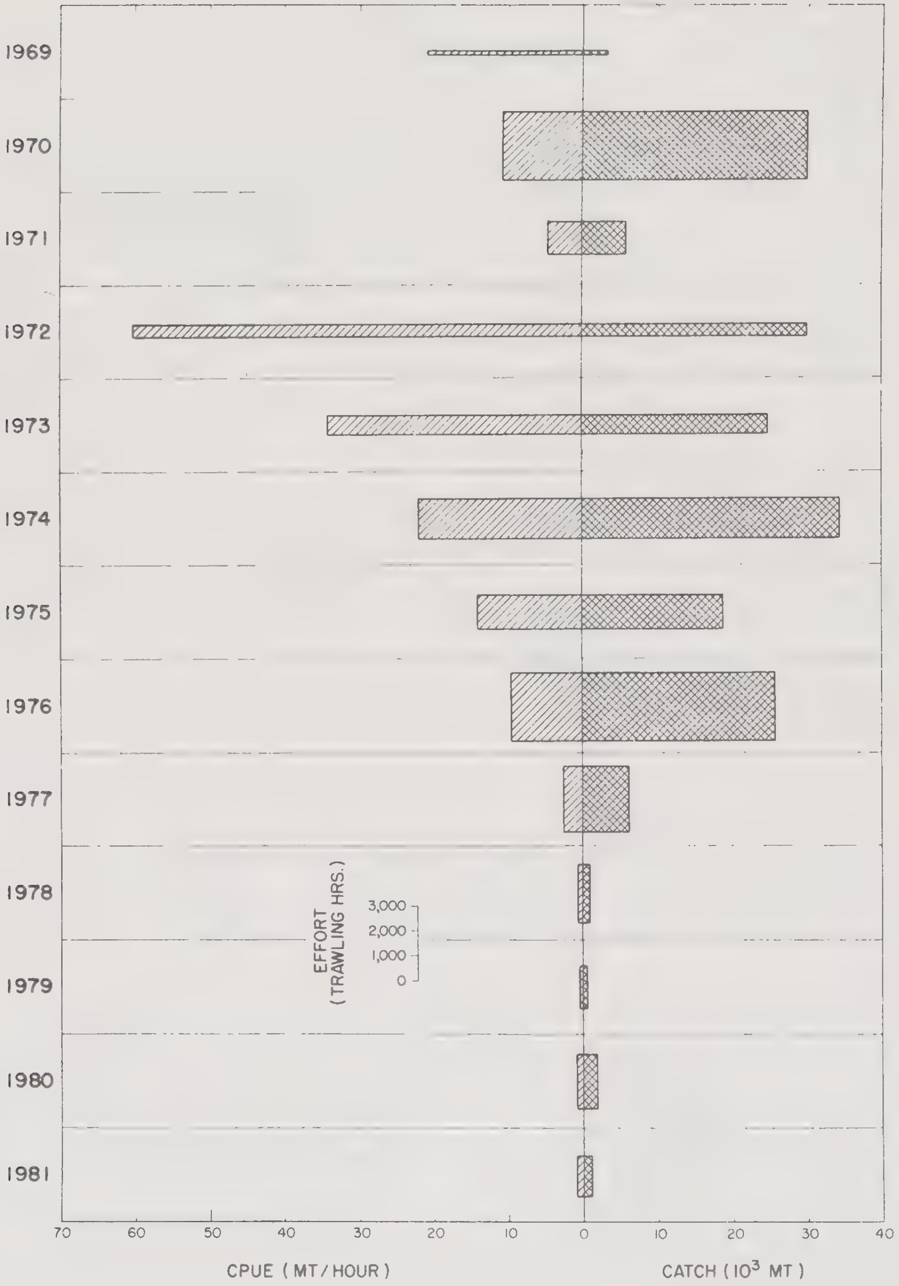


Figure 7. Three-way plot of yearly effort, catch, and catch per unit effort of pelagic armorhead from Japanese trawl fishery data; all seamounts combined

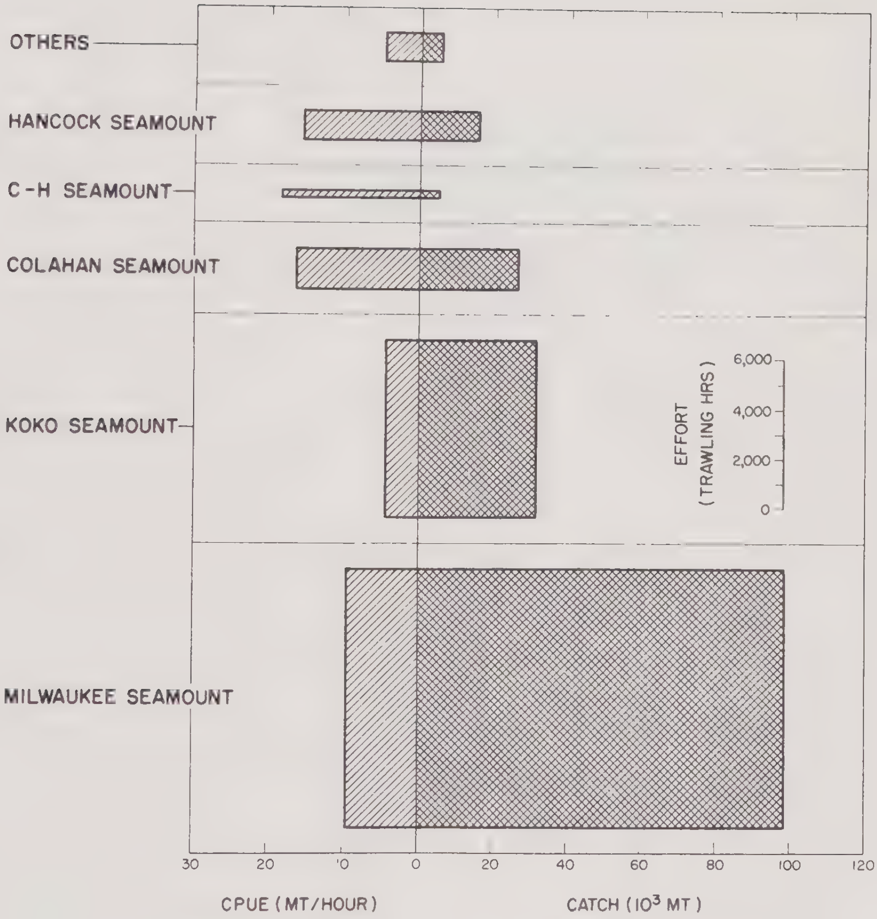


Figure 8. Three-way plot of effort, catch, and catch per unit effort of pelagic armorhead from Japanese trawl fishery data; years 1969-81 combined

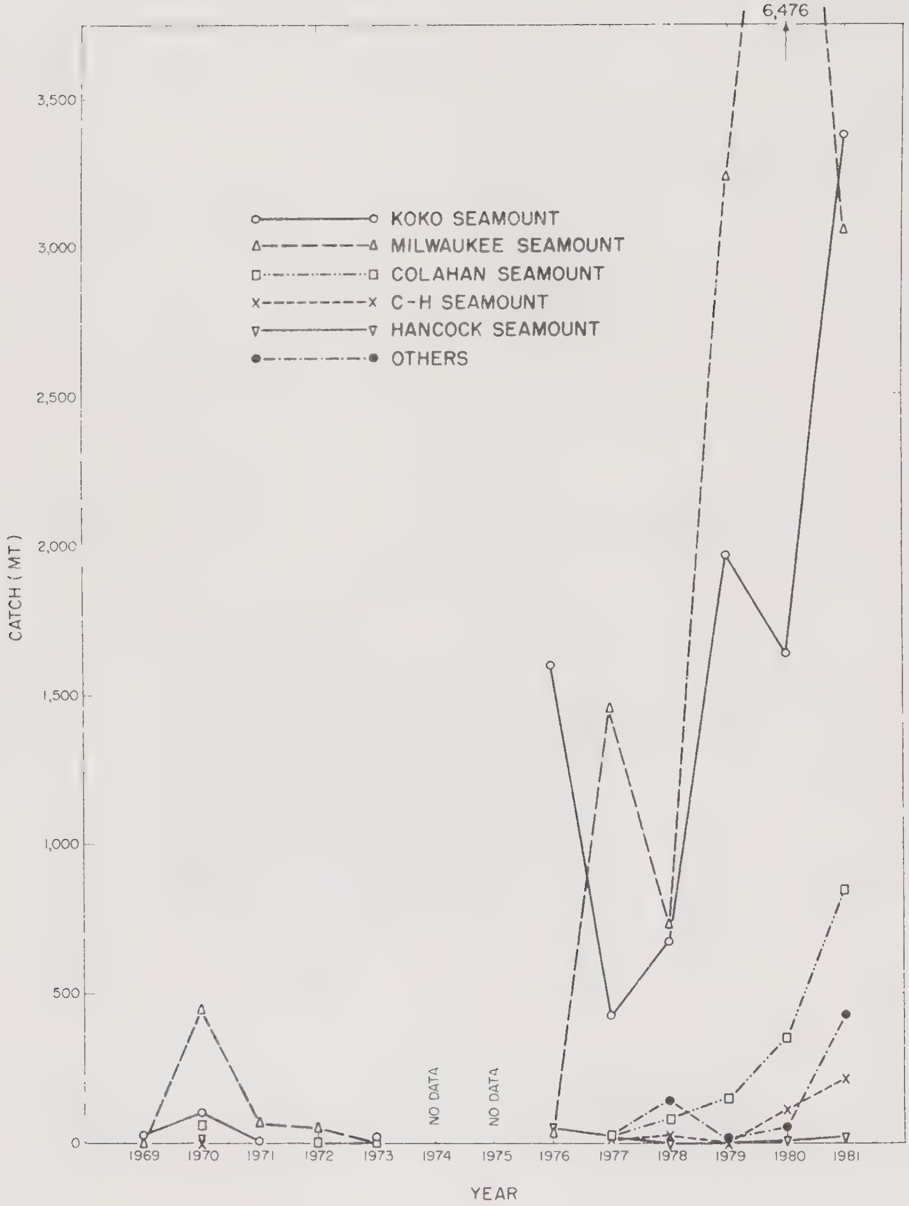


Figure 9. Yearly catch of alfonsin taken by Japanese trawlers at six seamounts within the Emperor-Hawaiian Ridge

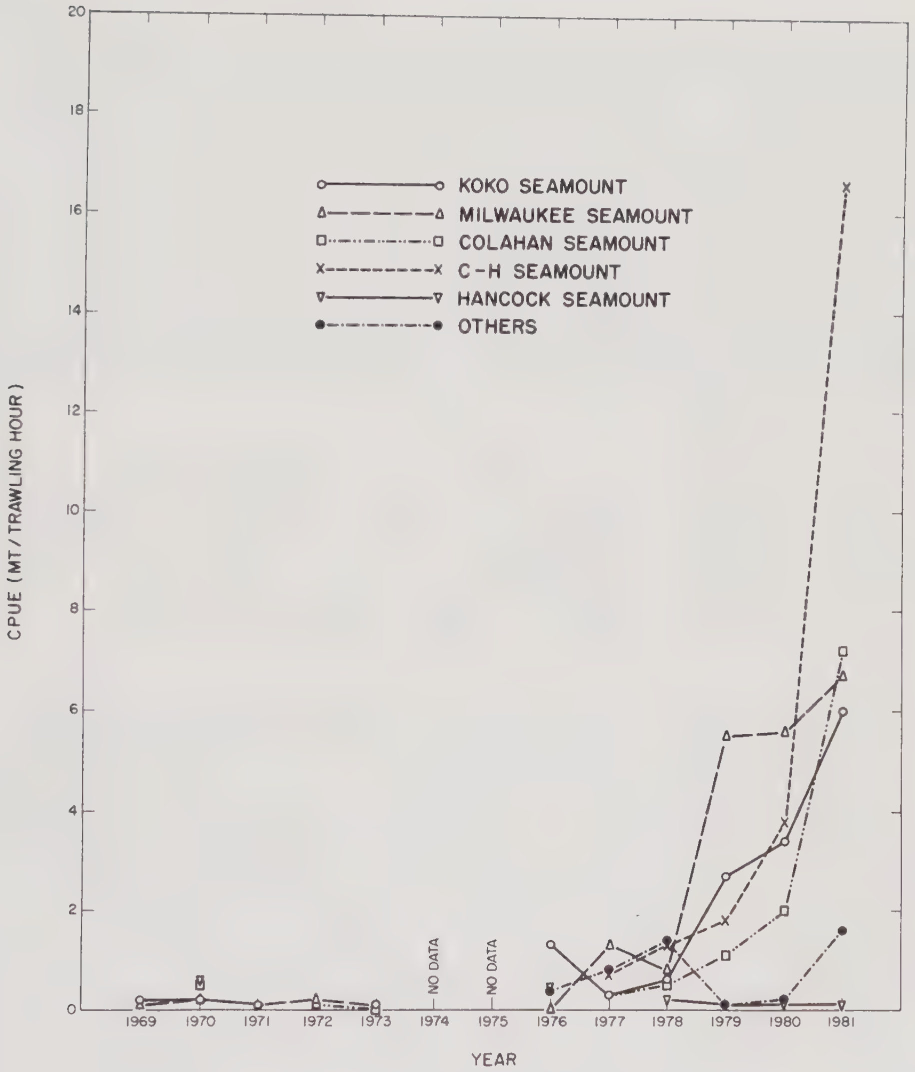


Figure 10. Yearly catch per unit effort of alfonsin taken by Japanese trawlers at six seamounts within the Emperor-Hawaiian Ridge

The largest catches of alfonsin were made during 1980-81, accounting for 59.0 percent (16,558 MT) of a total 28,063 MT reportedly harvested throughout 1969-81. During 1969-76 before pelagic armorhead catches dropped at all seamounts, its contribution to the total catch (only pelagic armorhead and alfonsin are considered here) was 98.6 percent (173,430 MT) and alfonsin 1.4 percent (2,532 MT). For 1977-81, when catches of pelagic armorhead remained low, it accounted for only 29.5 percent (10,679 MT) of the total catch while alfonsin rose to 70.5 percent (25,531 MT). The effort expended during the two periods was 11,131 trawling hours for 1969-76 and 10,494 trawling hours for 1977-81. In 1969-81, the largest amount of alfonsin was taken at Milwaukee, contributing 55.4 percent (15,534 MT) toward the total catch. The effort expended there was 48.0 percent (10,373 hours) of a total 21,625 hours for all seamounts.

Like the Soviets, the Japanese also observed diurnal fluctuations in the CPUE of pelagic armorhead. Results of trawl survey work at Kammu, Colahan, and Hancock showed two peaks in CPUE over a 24-hour day (Kitani and Iguchi, 1974). The CPUE generally peaked between 0300 to 0700 and 1600 to 1800 hours. With the possible exception of the exploratory phase, it is assumed that trawl hauls were mostly made at night.

The inclusion of Hancock within the 200-mile U.S. fishery conservation zone (FCZ) in March 1977 placed management of the fishery resources there under jurisdiction of the United States. Regulations were implemented and an annual catch quota for bottom trawling and bottom longlining of 2,000 MT and a limit on effort of 60 vessel-days were set. A license and complete catch reports for each trip are also required. Another requirement is the placement of a U.S. fishery observer onboard all vessels permitted to operate within the FCZ. This latter requirement allowed an onsite inspection of this fishery and the opportunity to independently gather catch data. Japan's total yearly catch quota for all species (except for nonretention ones) at Hancock was 1,000 MT. During 1978-82, nine Japanese trawlers operated under permit at Hancock, each with a U.S. observer onboard. In 1977, Japanese trawlers fished Hancock only during the period before its inclusion in the FCZ. The number of Japanese trawlers that fished at Hancock was one each in 1978 and 1979, two each in 1980 and 1981, and three during 1982.

The effort data collected by U.S. observers[1] at Hancock during 1978-82 are not in agreement with published Japanese data which apparently exclude effort and catch at SE Hancock during

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[1] U.S. foreign observer reports for Japanese permit trawling at Hancock Seamounts during 1978-82 are available from Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812. They include reports on the *Ryuyo Maru No. 2*, *Aso Maru*, *Kitakami Maru*, and *Takachiho Maru*.

1978-81, thereby explaining the higher effort and catches reported by U.S. observers (Figure 11). Since no independent estimates of catch and effort exist for earlier fishing conducted at Hancock, it is not known whether earlier data were also excluded for SE Hancock. In addition, the trawler fishing at Hancock in 1978 used a different measure of effort from the conventional one, i.e., elapsed time the trawl net was submerged. Effort was therefore roughly adjusted using data from a comparable-sized Japanese trawler. These discrepancies probably account for the differences in effort, catch, and CPUE at Hancock during 1978. The other discrepancies for 1979-81 may solely result from the exclusion by the Japanese of SE Hancock from the Hancock category. Despite these discrepancies, observer data collected during 1978-82 show a similar sustained trend of low pelagic armorhead catches.

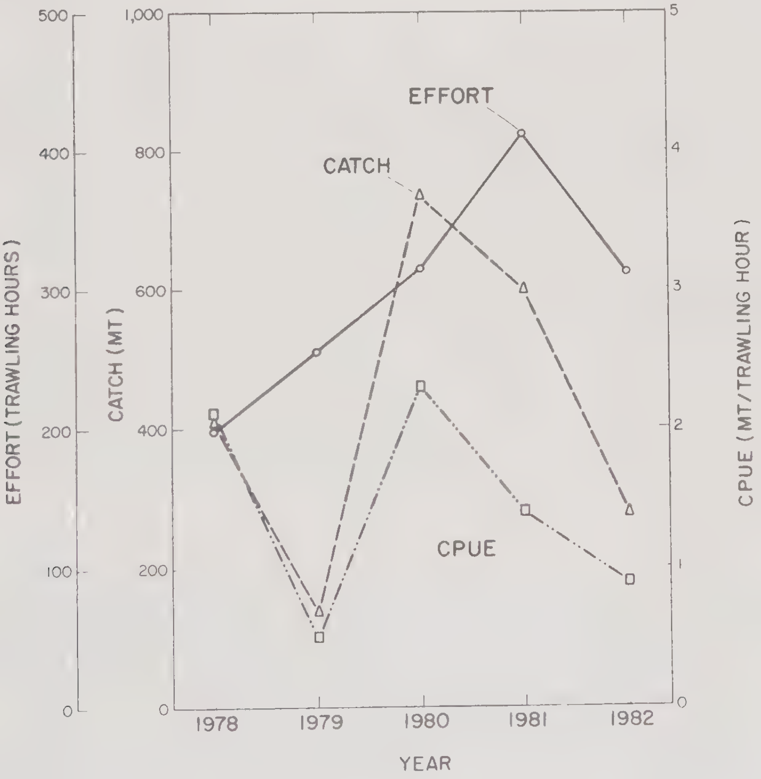

Figure 11. Yearly effort, catch, and catch per unit effort of pelagic armorhead taken by Japanese trawlers at Hancock Seamounts as determined by U.S. foreign observers

The observer data also show low alfonsin catches at Hancock during 1977-82, a trend apparent in earlier years (Figure 9) according to a report by Takahashi and Sasaki (1977). The 1982 observer data show a slight increase in catch and CPUE for alfonsin with less effort than that made in 1981 (Figure 12).

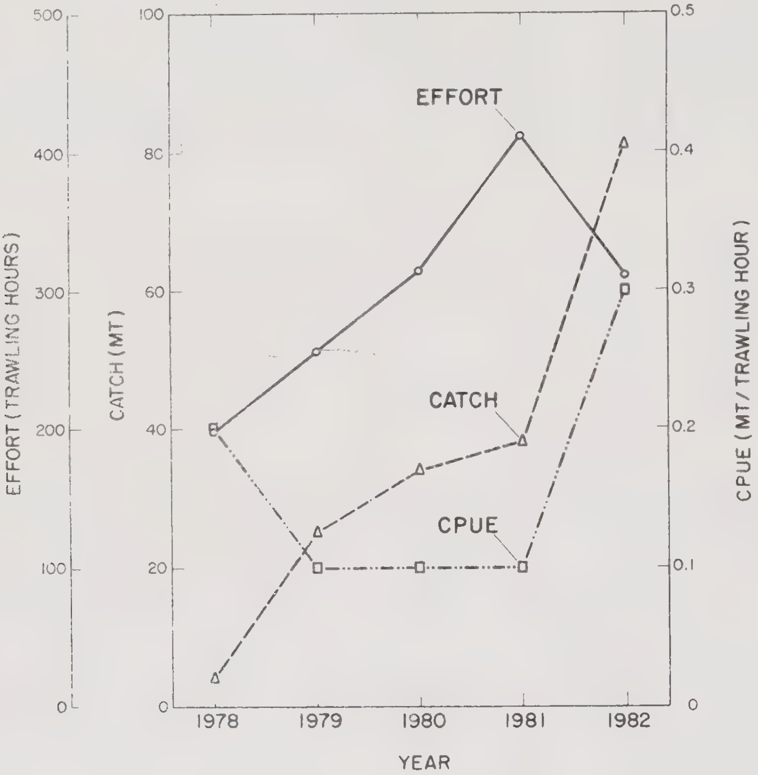

Figure 12. Yearly effort, catch, and catch per unit effort of alfonsin taken by Japanese trawlers at Hancock Seamounts as determined by U.S. foreign observers

Since 1976, the Southwest Fisheries Center Honolulu Laboratory of the National Marine Fisheries Service (NMFS) has made several very limited surveys of the fishery resources of the Emperor-Hawaiian Ridge seamounts as an adjunct to the tripartite and Sea Grant investigations of the Northwestern Hawaiian Islands (NWHI). Most of the effort was concentrated at Hancock. Because of differences in gear and technique, and the small amount of trawling effort, data from NMFS surveys are not directly comparable with the Japanese data. The NMFS surveys, however, were important as initial exploratory work and as a means for determining species composition of the seamount community and collecting samples for life history studies.

Besides trawling, NMFS investigated the Hancock summits with bottom handlines and traps. Bottomfishing was conducted primarily with 10-hook and 20-hook handline rigs powered by hydraulic gurdies. Catches consisted primarily of pelagic armorhead and spiny dogfish, _Squalus_ sp. At Koko, the handline catch consisted solely of the rockfish, _Helicolenus avius_. Trapping was also conducted at Hancock using a variety of fish traps. Catches were dominated by _Squalus_ sp. and pelagic armorhead was rare. Although catches of _Squalus_ sp. were relatively high from handline and trap fishing, they were incidental in the trawl catches.

OTHER SEAMOUNT FISHERIES

Bottom longlining

Although emphasis has been on trawl fishing, other fisheries operate on and around the seamounts. In 1972-73, a bottom longline fishery which primarily targeted alfonsin was initiated at Milwaukee. Other species caught in this fishery are _Hyperoglyphe japonica_, _Erilepus zonifer_, _Helicolenus avius_, and _Sebastes_ spp. (Sasaki, 1978). The gear is used to fish the summit and slopes and can be set in areas inaccessible to trawlers. I.I. Ikehara (1976: personal communication) reported that bottom longlining at Koko yielded an unspecified quantity of _E. zonifer_ at depths of 800 to 900 m. However, no catch and effort data on the seamount bottom longline fishery are available. An interview with one of the fishing masters revealed that catches of alfonsin and _Sebastes_ spp. were declining by 1976 and fewer Japanese vessels were fishing the area (Suisan Sekai, 1976). The fishing master also stated that a number of Korean vessels were involved in this fishery.

Gill netting

It was reported that 79 Taiwan gill net vessels began fishing in 1981 for the squid, _Ommatrephes bartramii_ (Suisan Sekai, 1981). Fishing was conducted in the area of the Emperor Seamounts. However, since no specific locations were given it is unknown whether this fishery included the southern Emperor Seamounts. These vessels were reportedly catching 3 to 6 MT per day. Approximately 200 Japanese squid jigging vessels and 200 gill net vessels were also operating on the Emperor Seamounts.

Other Taiwan vessels were reported to be fishing for saury, _Cololabis saira_, in the same area. It was reported that larval and juvenile saury are abundant in waters around the SE-NHR (Selitskaya, 1972).

Coral dragging

The first fishery resource to be discovered on the SE-NHR seamounts occurred in 1965 when Japanese fishermen found extensive beds of pink coral at Milwaukee. H. Ozawa (1970: personal communication) revealed that 113 MT of pink coral was harvested at Milwaukee in 1969 by Japanese fishermen. The harvesting method employed in this fishery involves the dragging of a weighted object across the bottom. Tangle nets attached to the weight collect the pieces of dislodged coral. This fishery apparently targets two species of pink coral: *Corallium secundum*, present at depths of 275 to 458 m, and *Corallium* sp. nov., found between 915 and 1,281 m.

Precious coral resources are present at seamount 10 (Grigg, 1974) and at Hancock although precious corals at the latter have apparently been harvested by foreign fishermen prior to 1977. With the advent of the 200-mile U.S. FCZ, foreign harvesting of precious corals and their retention through incidental catches by foreign trawlers or longliners, under permit to fish Hancock, are prohibited. However, R.W. Grigg (1983: personal communication) has found that 20 MT of precious corals were illegally harvested within the FCZ by foreign fishermen during 1980-82. During this time, about 600 MT of precious corals were harvested throughout the Emperor Seamounts by Japan and Taiwan. Reports from U.S. foreign observers[2] indicate few incidental trawl catches of precious corals occur at Hancock; all such catches are not retained.

ICHTHYOFAUNA OF THE SEAMOUNTS

During the early 1970s, Japanese efforts to expand the trawl fishery for pelagic armorhead extended to various seamounts located throughout the NWHI. Survey results showed a distinct change in the ichthyofauna at the seamounts located southeast of Hancock. The commercial and incidental species of the SE-NHR seamounts were absent from the predominantly subtropical ichthyofauna on the southern seamounts (Ladd, Nero, and seamounts 8 to 11). These results indicated a sharp demarcation of the ichthyofauna coinciding with the 180th meridian (Iguchi, 1973; Japan Marine Fishery Resource Research Center, 1973; Japan Fisheries Agency, 1974). Seamount survey data collected by NMFS, plus published information (Barsukov, 1973; Barsukov and Fedorov, 1975; Katayama, 1975; Chen, 1980: Nakaya et al., 1980; Kanayama, 1981; Borets, 1982; Dolganov, 1982; Parin and Mikhailin, 1982; Nakabo et al., 1983; Yabe, 1983) and a personal communication (I.I. Ikehara, 1976) have provided new records of the distribution of species (Table 1). The few species reported from Colahan and seamounts 10 and 11 reflect the small effort expended there. No data on C-H seamount are available.

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[2] See footnote 1

TABLE 1. DISTRIBUTION OF FISH SPECIES BY SEAMOUNT

Species	Family	KS	MS	CS	HS	SS	LS	NS	S9	S8
Neoscopelus microchir	Myctophidae	x								
Beryx splendens	Berycidae	x	x	x	x					
Beryx decadactylus	Berycidae	x	x	x	x					
Gephroberyx japonicus	Trachichthyidae	x	x		x					
Diretmus argenteus	Diretmidae	x								
Zenopsis nebulosa	Zeidae	x	x	x	x					
Psenopsis anomala	Centrolophidae	x								
Epigonus atherinoides	Apogonidae	x	x							
Sebastes flammeus	Scorpaenidae	x	x							
Podonema longipes	Moridae	x								
Macrorhamphosus scolopax	Macrorhamphosidae		x	x	x					
Ariomma lurida	Nomeidae				x					
Antigonia rubescens	Antigoniidae		x		x					
Helicolenus avius	Scorpaenidae	x	x							
Halargyreus sp.	Moridae		x							
Lophiodes miacanthus	Lophiidae		x	x	x					
Scomber japonicus	Scombridae				x					
Chascanopsetta prorigera	Bothidae		x		x					
Lotella maximowiczi	Moridae		x							
Erythrocles scintillans	Emmelichthyidae				x					
Dalatias licha	Squalidae		x							
Nansenia ardesiaca	Bathylagidae		x							
Gonostoma elongatum	Gonostomatidae		x							
Maurolicus muelleri	Gonostomatidae		x							
Astronesthes ijiami	Astronesthidae		x							
Chauliodus sloani	Chauliodontidae		x							
Chlorophthalmus albatrossis	Chlorophthalmidae		x							
Coelorhynchus sp.	Macrouridae		x							
Trachipterus iris	Trachipteridae		x							
Malthopsis tiarelle	Ogcocephalidae		x							
Chaunax fimbriatus	Chaunacidae		x							
Parabothus coarctatus	Bothidae		x		x					
Microstomus pacificus	Pleuronectidae		x							
Bembradium roseum	Platycephalidae		x							
Foetorepus kamuensis	Callionymidae		x							
Peristedion engyceros	Peristediidae		x		x					
Lepidopus calcar	Trichiuridae		x							
Benthodesmus tenuis	Trichiuridae		x							
Anthias rubromaculatus	Serranidae		x							
Chimaera owstoni	Chimaeridae	x								
Helicolenus sp.	Scorpaenidae	x								
Hozukius guyotensis	Scorpaenidae	x	x							
Adelosebastes latens	Scorpaenidae	x								
Caprodon unicolor	Serranidae					x				
Lepidion inosimae	Moridae	x								
Lepidion schmidti	Moridae	x								
Marukawichthys pacificus	Ereuniidae	x								
Pentaceros japonicus	Pentacerotidae		x							
Plectranthias kelloggi	Serranidae		x		x					
Grammatonotus laysanus	Serranidae		x		x					
Bembrops filifera	Bembropsidae		x							
Rhynchocymba nystromi nystromi	Congridae				x					
Symphysanodon typus	Lutjanidae				x					
Antigonia steindachneri	Antigoniidae				x					
Emmelichthys struhsakeri	Emmelichthyidae				x					
Neopercis roseoviridis	Mugiloididae				x					

TABLE 1. DISTRIBUTION OF FISH SPECIES BY SEAMOUNT (continued)

Species	Family	KS	MS	CS	HS	SS	LS	NS	S9	S8
Etmopterus pusillus	Squalidae				x					
Isistius brasiliensis	Squalidae				x					
Argyropelecus aculeatus	Sternoptychidae				x					
Symphysanodon maunaloae	Lutjanidae				x					
Astronesthes lucifer	Astronesthidae				x					
Arnoglossus debilis	Bothidae				x					
Ruvettus pretiosus	Gempylidae				x					
Argyripnus atlanticus	Gonostomatidae				x					
Hoplichthys sp.	Hoplichthyidae				x					
Physiculus edelmanni	Moridae				x					
Myctophum nitidulum	Myctophidae				x					
Diaphus trachops	Myctophidae				x					
Parapercis multifaciata	Mugiloididae				x					
Tosanoides filamentosus	Serranidae				x					
Meadia abyssalis	Synaphobranchidae				x					
Glossanodon struhsakeri	Argentinidae				x					
Dasyatis matsubarai	Dasyatidae				x					
Echinorhinus cookei	Squalidae		x							
Paratrachichthys sp.	Trachichthyidae		x							
Etmopterus villosus	Squalidae				x					
Helicolenus fedorovi	Scorpaenidae	x								
Lepidopus lex	Trichiuridae		x							
Laemonema rhodochir	Moridae				x					
Stethopristes eos	Zeidae				x					
Hoplostethus mediterraneus	Trachichthyidae				x					
Prionace glauca	Carcharhinidae				x					
Hexanchus griseus	Hexanchidae				x					
Chlorophthalmus oblongus	Chlorophthalmidae				x					
Hollardia goslinei	Triacanthidae				x					
Brama orcini	Bramidae				x					
Alopias sp.	Alopiidae				x					
Erilepis zonifer	Anoplopomatidae	x								
Centroscyllium nigrum	Squalidae				x					
Decapterus tabl	Carangidae				x		x			
Hyperoglyphe japonica	Centrolophidae	x	x	x	x		x			
Cookeola boops	Priacanthidae				x	x	x	x		x
Antigonia eos	Antigoniidae	x	x	x	x	x				
Physiculus grinelli	Moridae				x		x	x		
Squalus sp.	Squalidae	x	x		x	x	x	x		
Promethichthys prometheus	Gempylidae				x		x	x		
Pentaceros richardsoni	Pentacerotidae	x	x	x	x		x			
Polymixia berndti	Polymixiidae	x	x		x			x		
Fistularia villosa	Fistulariidae						x			
Velifer multispinosus	Veliferidae						x			
Decapterus sp. (not *tabl*)	Carangidae						x			
Pseudocaranx dentex	Carangidae						x	x	x	
Seriola aureovittata	Carangidae						x		x	
Upeneus sp.	Mullidae						x			x
Pseudupeneus sp.	Mullidae									x
Bleekeria sp.	Ammodytidae						x			
Carapus sp.	Carapidae									x
Chaetodon miliaris	Chaetodontidae						x			x
Chaetodon fremblii	Chaetodontidae						x			x
Lactoria sp.	Ostraciontidae						x			
Canthigaster cinctus	Canthigasteridae									x
Amanses sp.	Balistidae						x			

TABLE 1. DISTRIBUTION OF FISH SPECIES BY SEAMOUNT (continued)

Species	Family	KS	MS	CS	HS	SS	LS	NS	S9	S8
Pristipomoides filamentosus	Lutjanidae							x	x	x
Caranx delicatissimus	Carangidae									x
Naso unicornis	Acanthuridae									x
Priacanthus meeki	Priacanthidae					x				
Caprodon schlegelii	Serranidae					x				
Dendrochirus barberi	Scorpaenidae									x
Cheilodactylus vittatus	Cheilodactylidae									x
Congrina aequoria	Congridae						x			
Ariosoma marginatum	Congridae						x			
Etelis carbunculus	Lutjanidae						x	x	x	x
Gymnothorax steindachneri	Muraenidae						x	x		
Gymnothorax berndti	Muraenidae						x			
Epinephelus quernus	Serranidae					x	x	x	x	x
Seriola dumerili	Carangidae							x	x	x
Gymnothorax undulatus	Muraenidae							x		
Conger oligoporus	Congridae					x				
Caranx ignoblis	Carangidae									x
Pristipomoides zonatus	Lutjanidae								x	x
Pristipomoides sieboldii	Lutjanidae						x	x	x	
Etelis coruscans	Lutjanidae						x		x	
Pontinus macrocephalus	Scorpaenidae						x	x	x	
Sphoeroides cutaneus	Tetraodontidae						x			
Bodianus vulpinus	Labridae							x		

Note: KS = Koko Seamount; MS = Milwaukee Seamount Group; CS = Colahan Seamount; HS = Hancock Seamounts; SS = Seamounts 10 and 11; LS = Ladd Seamount; NS = Nero Seamounts; S9 = Seamount 9; S8 = Seamount 8

Most fishes occurring on the summit of northern seamounts are deep-water, benthic-demersal forms. The predominance of these types is hardly surprising since the collections were derived almost solely from bottom trawls. Some mesopelagic types were also collected, although it is uncertain whether these species were collected in the water column above the seamount or represent mesopelagic species which exhibit more demersal affinities. Most fishes collected from the northern seamounts were small and of no commercial value. Of the 80 fish species found only among the northern seamounts, more than 50 percent are known to occur elsewhere within the Hawaiian archipelago. Table 1 also shows that 9 of the 90 species found at the northern seamounts are distributed beyond the 180th meridian. Most of the transitional species occurred at Ladd and Nero Seamounts. Two of them, *Hyperoglyphe japonica* and pelagic armorhead, have distributions centered in the northern seamounts. Only one specimen of *H. japonica* and two of pelagic armorhead were taken within the southern seamounts. The remaining seven transitional species are known from elsewhere in the Hawaiian archipelago.

Apart from the transitional species, subtropical reef fishes and members of the commercially important snapper-grouper complex characterize the ichthyofauna of the southern seamounts. Seamounts 10 and 11 may be exceptions. Although these new results confirm a distinct ichthyofaunal change near the 180th meridian, the ichthyofauna of Ladd and Nero (and probably seamounts 10 and 11) may be of a more transitional nature than originally thought. Since most of the fishes inhabiting the northern seamounts occur elsewhere in the deeper waters of the Hawaiian Archipelago, the shallower summits and warmer temperatures characteristic of southern seamounts apparently offer an unsuitable habitat for these species.

LIFE HISTORY OF TARGET SPECIES

Pelagic armorhead

Distributional information on the smallest reported sizes of pelagic armorhead came from results of Soviet ichthyoplankton surveys over the SE-NHR seamounts in 1969 and 1976 (Borets, 1979). These specimens ranged from 5 to 20 mm long and occurred more frequently south of 33°N. The egg, larval, and juvenile stages inhabit the surface layers and their distribution is subject to the meanderings of the surface currents (Borets, 1979). The first report of a juvenile was a 35-mm specimen collected off Cape Horn, South America and was initially given the name Pentaceros kneri by Steindachner in 1866 (Smith, 1964). Since then, juveniles have been collected off New Zealand (Smith, 1964), from south of the Aleutian Islands (Honma and Mizusawa, 1969; Randall, 1980), and off Gough Island in the southeast Atlantic (Borets, 1980).

Pelagic armorhead was first described in 1844 from a 530-mm adult specimen taken in deep water off Cape Point, South Africa (Smith, 1964). Adults are known elsewhere in the southeast Atlantic from Valdivian Seamount in the Walvis Ridge area (Borets, 1980). In the Pacific, adults are known from both hemispheres. Besides the large population inhabiting the SE-NHR seamounts, adults also occur at Mellish Bank (Takahashi and Sasaki, 1977) and at Ladd Seamount and Kure Atoll (from a single specimen collected at each) (Randall, 1980). In Japanese waters, adults occur around the Boso Peninsula (Abe, 1957) and off Hachijo Island and the Ogasawara Islands (Abe, 1969; Zama et al., 1977b). A few adult specimens have also been collected in waters along western North America from British Columbia (Welander et al., 1957; Clemens and Wilby, 1961; Hart, 1973), Oregon (Wagner and Bond, 1961), and California (Follett and Dempster, 1963; Smith, 1965). Adults and juveniles also inhabit waters south of the Aleutian Islands and around the Gulf of Alaska in the northeast Pacific (Welander et al., 1957; Chikuni, 1970). In the South Pacific, the Soviets collected five adult specimens from one of the seamounts located on the Sala y Gomez Ridge in the vicinity of Easter Island (Borets, 1980). The Japanese obtained three large adults off the east coast of Australia at Derwent Hunter Seamount.

Apparently, pelagic armorhead in the Pacific have an antitropical distribution. The lowest latitudinal records are at Kure Atoll (lat. 28°30.82'N, long. 178°20.86'W) in the North Pacific (Randall, 1980) and Sala y Gomez Ridge (lat. 24°57'S, long. 97°41'W) in the South Pacfic (Borets, 1980). A preliminary effort to locate pelagic armorhead in the Hawaiian islands (lat. 20° to 22°N) was unsuccessful (Okamoto, 1982). Borets (1980) recognized two distributional centers of reproductive adults: the SE-NHR seamounts and Walvis Ridge. Aside from these areas, "good" fishing grounds were reported near Hachijo Island (Abe, 1969). A number of pelagic armorhead have also been caught in oceanic waters of the northeastern Pacific by Japanese whaling ships. These fish were taken by night handlining at the surface under ship's lights. They have also been found in the stomachs of sei whales captured from this area (Chikuni, 1970; Sasaki, 1974). The presence of large numbers of pelagic armorhead in sei whale stomachs infers an epipelagic existence in these waters since these whales are known to preferentially feed on surface-dwelling fish (Chikuni, 1970).

Pelagic armorhead in the northeast Pacific are known only from surface or nearsurface waters during June-September (Welander et al., 1957; Honma and Mizusawa, 1969; Chikuni, 1970; Randall, 1980). Pelagic armorhead school in the surface waters of the northeast Pacific during daylight and nondaylight hours. Among the SE-NHR seamounts, pelagic armorhead are commercially taken from depths of 200 to 490 m (Takahashi and Sasaki, 1977). Aggregations of pelagic armorhead have been recorded on the slopes of seamounts at the 800- to 900-m depth (Sakiura, 1972; Borets, 1980). Chikuni (1970, 1971) suggested that the horizontal and vertical distribution of pelagic armorhead is correlated with a certain temperature range. He surmised that the absence of pelagic armorhead during northeast Pacific winters indicated a lower tolerance limit of 5°C, and that their year-round occurrence on the SE-NHR seamounts and during summer in the northeast Pacific suggested an upper limit of 15° to 20°C. Chikuni suggested a preferred range of 8°to 15°C and reasoned that their absence on the Emperor Seamounts north of Koko (depths of 1,000 m or more) and on Hawaiian Ridge seamounts east of the 180th meridian (shallow summits) was due to intolerably low and high temperatures, respectively.

As stated earlier, the catches of pelagic armorhead vary diurnally on the seamounts. The Soviets report that this is due to a vertical migration upwards from the summit as daylight approaches and a descent to the summit at dusk. The fish remain on the summit during darkness and in the upper water layers (80- to 100-m depth) during daylight (Sakiura, 1972). Barnett[3] reported a correlation between poor night catches and shipboard fish finders showing concentrations of fish (presumed to be pelagic armorhead) at levels either above or beyond the summit. A variation of the hypothesis reported by Sakiura was proposed by Kitani and Iguchi (1974). They agreed that the fish rise off the summit during daylight, but they also maintain that the fish descend past the summit during the night. Consequently, it was felt these fish pass through the summit level twice during the night: once after dusk and again before dawn. Both Soviet and Japanese investigators suggest that these vertical movements are related to the foraging activity of pelagic armorhead. Soviet results (Sakiura, 1972) indicate that pelagic armorhead preferentially feed during daylight, especially between 0800 and 1000, and feed little or not at all during the night. The findings of Kitani and Iguchi (1974) are contrary to Soviet results since they found a higher proportion of stomachs with food between midnight and dawn. However, field observations by U.S. foreign observers[4] indicate that feeding takes place only during daylight, primarily in the morning and late afternoon.

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[3] See footnote 1, specifically W.B. Barnett, 1981, Southwest Fisheries Center Administrative Report H-81-9.

The Soviets report that surface-dwelling crustaceans are important prey items of pelagic armorhead (Sakiura, 1972). A portion of the diet consists of deep-scattering layer organisms (Sasaki, 1974). Prey items are primarily amphipods, copepods, pteropods, euphausiids, sergestids, macrura, tunicates, and myctophids. Borets (1979) reported that juveniles feed on smaller plankters, particularly copepods, whereas adults prey chiefly on tunicates, euphausiids, and mesopelagic fishes. Stomach contents examined during a Japanese survey cruise consisted of copepods, krill, mysids, myctophids, and other mesopelagic fishes (Japan Fisheries Agency, 1974). Chen (1980) found two species of red deepsea shrimp to be the principal prey of pelagic armorhead taken at Kammu. The U.S. foreign observers[5] identified amphipods, copepods, euphausiids, salps, shrimps, myctophids, and other small fishes as principal prey items.

The spawning season of pelagic armorhead at the SE-NHR seamounts has been determined from several sources (Japan Fisheries Agency, 1974; Sasaki, 1974; Bilim et al., 1978; Borets, 1979) to extend from December to March. Spawning peaks during January-February. The proportion of spent individuals increases from February to March although some ovaries were found in a pre-spawning condition in March (Sasaki, 1974). The U.S. foreign observers[6] found most females in an early developing stage during April-June whereas Chen (1980) found well-developed ovaries in

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[4] See footnote 1, specifically T.K. Kazama, 1978, Southwest Fisheries Center Administrative Report 15H, 1978 and W.B. Barnett, 1982, Southwest Fisheries Center Administrative Report H-82-21.

[5] See footnote 1

[6] See footnote 1, specifically T.K. Kazama, 1978, Southwest Fisheries Center Administrative Report 15H, 1978 and W.B. Barnett, 1982, Southwest Fisheries Center Administrative Report H-82-12.

May. Soviet investigators found ovaries in an early developmental stage in summer and fall; moderate development began in September (Sakiura, 1972). Pre-spawning conditions were present among some females in mid-November (Bilim et al., 1978). No eggs were collected in plankton tows over the seamounts during spring; however, large numbers of juveniles were reported in March-April (Sakiura, 1972; Sasaki, 1974).

Fecundity estimates for 30-cm females of pelagic armorhead from three SE-NHR seamounts ranged from 99,000 to 110,000 eggs (Borets, 1979). Studies by Bilim et al. (1978) indicate that during spawning, eggs are released in four to six batches. Chikuni (1970) reported that 6-year-old fish are sexually mature and suggested that first maturity occurs at an earlier age. Age estimates of 3 years for 22-cm fork length (FL) and 6 years for 32-cm FL fish were determined by annular ring counts on scales. Chikuni estimated the age groups of pelagic armorhead taken in the trawl fishery (mean FL of 30.0 cm) are 5 to 7 years old. Results of spectrophotometric analysis on scales by Vasil'kov and Borets (1978) and information reported by Borets (1979) indicate ages of 6 to 8 years for 26- to 30-cm fish.

A growth of 7.5 cm in 3 years (from an initial length of 25.4 cm) was reported by Hart (1973) for a pelagic armorhead held in captivity at Vancouver Aquarium, British Columbia. However, yearly increment growth data indicate that a growth of 7.5 cm in the wild (from a similar initial length) requires more than 4 years (Borets, 1979). Borets showed a 7.5 to 7.7 cm growth from age 0 to 1 and growth between subsequent year classes decreasing to 1.0 to 1.4 cm from age 9 to age 10. At present, NMFS is conducting an otolith analysis to determine age and growth.

A perplexing aspect of pelagic armorhead biology is the presence of morphological variants among adults on the SE-NHR seamounts (Figure 2). A number of reports (Japan Fisheries Agency, 1974, Sasaki, 1974; Takahashi and Sasaki, 1977; Chen, 1980) have commented on this variation and recognized two or three types. Observations by NMFS personnel on Townsend Cromwell research cruises and on foreign vessels indicate three types of pelagic armorhead based on body depth and color. The "lean" type is more elongate and is brown to brownish-gray. The "fat" type has a relatively greater body depth, somewhat "square-shaped," with a bluish dorsal region and a white ventral region. An "intermediate" type has a body depth in-between the other types and a lean type coloration. It has also been noted by NMFS researchers and Takahashi and Sasaki (1977) that certain lean types captured at Hancock appear rather emaciated, with skin that is easily ruptured. Gonads are poorly developed in these fish and the viscera discolored. All of these apparent abnormalities indicate an unhealthy condition. These fish also lack fat deposits in the visceral cavity and other lean fish had limited amounts. Fat types and intermediate types to a lesser degree have large fat deposits in the visceral cavity.

All three types of pelagic armorhead are found within the SE-NHR seamounts although lean and intermediate types predominate in the catches. The fat types are relatively rare in the trawl catches on the seamounts. However, only the fat types have been found in the northeast Pacific. The distribution and coloration of fat types suggest a primarily epipelagic existence.

The variability in body type of adult pelagic armorhead is apparently absent in the juveniles. Photographs of juveniles appearing in Smith (1964) and Honma and Mizusawa (1969) show them to be relatively deep bodied with a mottled coloration, primarily in the dorsal region. Juveniles of a congeneric, P. japonicus, show similar coloration during the epipelagic phase. This coloration eventually disappears when juveniles shift to a deeper demersal existence (Zama et al,, 1977a).

To better define the nature and significance of the variations between types, a preliminary morphometric and meristic study was begun at NMFS. A breakdown of the sample size according to seamount, sex, and type appears in Table 2. The morphometrics and meristics of specimens by seamount, sex, and type are shown in Table 3. The means were analyzed within each of the three sources (plus their four possible combinations) using a three-way univariate ANOVA (Statistical Analysis System, 1979) (Table 4).

Highly significant differences within sex and type occur among all morphometric variables measured. However, there is also a significant sex-type interaction which probably influenced the results within each of the two previous sources. The sample sizes shown in Table 2 indicate that the lean sample was dominated by males, whereas in the intermediate sample, females predominated. Sex-type differences in body length may also have influenced the results. Maximum body depth is plotted against standard length by sex in Figure 13 and by body type in Figure 14. Aside from the sex and type variation in body depth, these plots also indicate that the males and lean types were smaller compared with females and intermediate types. Whether these tendencies within the sample accurately reflect the seamount population of pelagic armorhead is unknown. In light of probable interactive effects and possible sample bias, the results for sex and type are inconclusive. Results of the seamount-sex and seamount-type comparisons indicate that each particular sex and type alone are not significantly different morphometrically between seamounts. However, there were significant differences, especially in weight, between pelagic armorhead of different seamounts. Borets (1979) presented results of a morphometric study indicating no significant differences among samples of pelagic armorhead taken at four seamounts within the SE-NHR area.

TABLE 2. SAMPLES OF PELAGIC ARMORHEAD USED IN MORPHOMETRIC AND MERISTIC STUDIES

Specimen	SE Hancock	NW Hancock	C-H	All Three Seamounts Combined
Leans				
Female	11	19	24	54
Male	28	27	32	87
Total	39	46	56	141
Intermediates				
Females	32	44	31	107
Male	26	7	10	43
Total	58	51	41	150
Fats				
Females	7	2	0	9
Male	13	6	0	19
Total	20	8	0	28
Total by Sex				
Female	50	65	55	170
Male	67	40	42	149
TOTAL	117	105	97	319

The meristic results shown in Table 4 do not separate the three body types. Borets (1979) presented similar meristic results for four seamounts although no comparisons were made for sex, type, and their possible combinations. These meristic results are of interest because of speculation on whether the types represent genetically distinct species or subspecies. To better address this question, tissue samples from these types were collected for electrophoretic analysis; results are not yet available. An earlier electrophoretic study on 10 protein systems from samples collected at four SE-NHR seamounts detected no genetic differences in fish (Borets, 1979).

The ecological significance of the different body types is little understood. Borets (1980) reported that the young are pelagic until a certain size and later shift to a demersal habitat, especially over the seamounts. This shift occurs around age 7, which corresponds to the sizes constituting the bulk of pelagic armorhead taken in the trawl fishery. Borets, however, makes no specific mention of polymorphic variation in relation to the habitat change.

TABLE 3. MEAN VALUES DERIVED FROM THE MORPHOMETRICS AND MERISTICS STUDY OF PELAGIC ARMORHEAD

Characteristic	Location			Sex		Type		
	SE Hancock	NW Hancock	C-H	Female	Male	Lean	Intermediate	Fat
Morphometric								
Weight (g)	503.3	514.8	455.0	543.7	433.4	385.3	573.3	590.3
Standard Length (mm)	255.8	256.7	255.3	262.8	248.1	246.6	265.1	253.8
Fork Length (mm)	295.9	298.5	296.8	304.7	288.3	287.0	307.0	295.8
Greatest Orbit Length (mm)	24.1	24.5	25.0	24.7	24.3	25.0	24.5	22.6
Least Interorbital Length (mm)	26.5	26.7	25.5	27.1	25.4	24.7	27.5	28.1
Snout Length (mm)	32.3	32.3	31.9	33.2	31.1	30.6	33.5	33.0
Head Length (mm)	84.2	84.7	84.4	86.5	82.1	81.8	87.0	83.5
Predorsal Length (mm)	103.7	103.2	102.0	105.8	99.9	98.1	106.9	106.8
Predorsal to Prepelvic Length (mm)	96.4	94.8	91.7	97.9	90.4	85.4	100.7	105.6
Maximum Body Depth (mm)	94.0	92.3	89.2	95.5	88.0	82.9	98.2	103.5
Meristics								
Lateral Line Scales in Standard Length	72.9	73.1	72.1	72.8	72.7	72.7	72.8	72.5
Upper Gill Rakers on First Arch	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.5
Lower Gill Rakers on First Arch	17.8	17.8	17.6	17.7	17.8	17.7	17.7	17.8
Dorsal Spines	13.9	13.9	13.9	13.9	13.9	13.8	13.9	13.9
Anal Spines	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0
Dorsal Soft Rays	8.9	8.8	8.8	8.8	8.9	8.9	8.8	8.9
Anal Soft Rays	7.3	7.4	7.4	7.4	7.4	7.4	7.3	7.4
Pectoral Rays	17.8	17.7	17.7	17.7	17.7	17.7	17.8	17.7
Precaudal Vertebrata	12.0	12.0	12.0	12.0	12.0	12.0	12.0	12.0
Caudal Vertebrata	12.9	13.0	12.9	13.0	12.9	12.9	12.9	13.0
Total Vertebrata	25.0	25.0	24.9	25.0	25.0	25.0	25.0	25.0

TABLE 4. RESULTS OF ANOVA ON MORPHOMETRIC AND MERISTIC DATA FROM PELAGIC ARMORHEAD

Characteristic	Seamount	Sex	Type	Seamount x Sex	Sex x Type	Seamount x Type	Seamount x Sex x Type
Degrees of Freedom	2	1	2	2	2	3	3
Morphometric							
Weight (g)	**	***	***	NS	***	NS	*
Standard Length (mm)	NS	***	***	NS	**	NS	*
Fork Length (mm)	NS	***	***	NS	**	NS	*
Greatest orbit Length (mm)	*	***	***	NS	*	*	NS
Least Interorbital Length (mm)	*	***	***	NS	***	NS	*
Snout Length (mm)	NS	***	***	NS	NS	NS	NS
Head Length (mm)	NS	***	***	NS	**	NS	*
Predorsal Length (mm)	NS	***	***	NS	***	NS	NS
Predorsal to Prepelvic Length (mm)	NS	***	***	NS	***	NS	NS
Maximum Body Depth (mm)	NS	***	***	NS	***	NS	NS
Meristic							
Lateral Line Scales in Standard Length	NS	NS	NS	NS	NS	NS	NS
Upper Gill Rakers on First Arch	NS	NS	NS	NS	NS	NS	NS
Lower Gill Rakers on First Arch	NS	*	NS	NS	*	NS	NS
Dorsal Spines	NS	NS	NS	NS	NS	NS	NS
Anal Spines	NS	NS	NS	NS	NS	NS	NS
Dorsal Soft Rays	NS	NS	NS	NS	NS	NS	NS
Anal Soft Rays	NS	NS	NS	NS	NS	NS	NS
Pectoral Rays	NS	NS	NS	NS	NS	NS	NS
Precaudal Vertebrata	NS	NS	NS	NS	NS	NS	NS
Caudal Vertebrata	NS	NS	NS	NS	NS	NS	NS
Total Vertebrata	NS	NS	NS	NS	NS	NS	NS

Note: NS = $P > 0.05$; * = $0.01 < P \leq 0.05$; ** = $0.001 < P \leq 0.01$; *** = $P \leq 0.001$

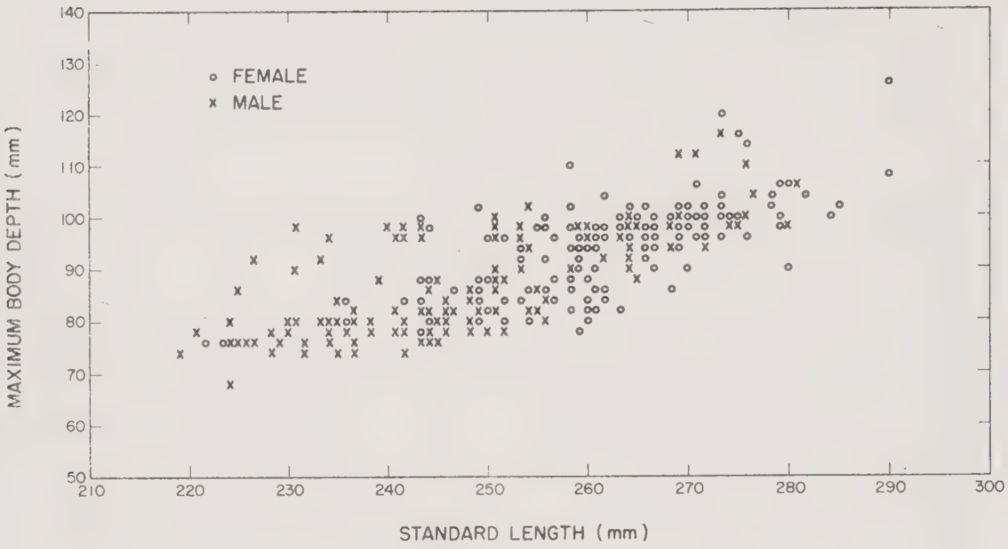

Figure 13. Relationship between maximum body depth and standard length, by sex, for pelagic armorhead

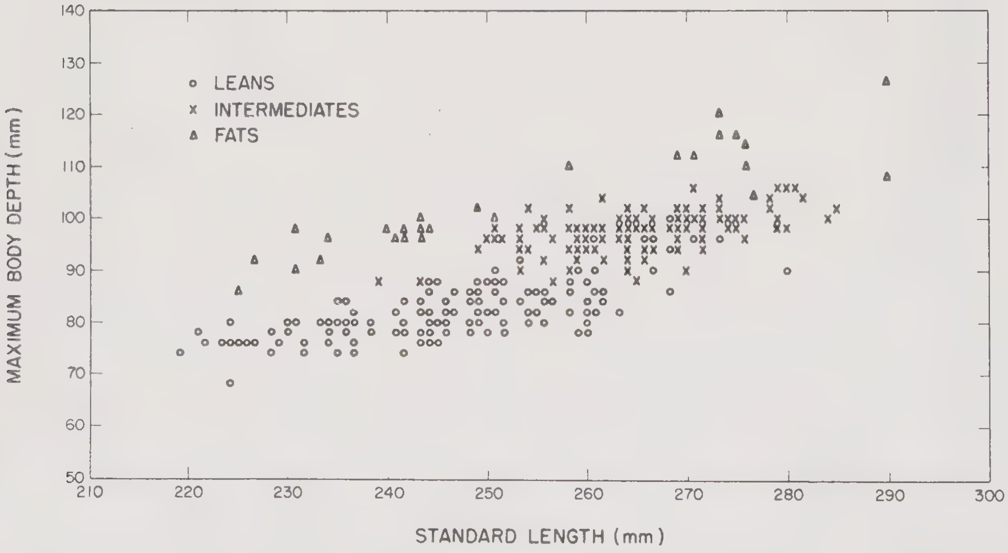

Figure 14. Relationship between maximum body depth and standard length, by body type, for pelagic armorhead

The annual mean FL of pelagic armorhead pooled for all seamounts is available from 1969 to 1976 (Takahashi and Sasaki, 1977) and for 1977-79 and 1981 (Sasaki, unpublished data) (Table 5). For 1972, the mean FL was apparently smaller than earlier and succeeding years. Perhaps coincidentally, the CPUE for 1972 was the highest recorded for three of the seamounts, and the CPUE was higher at the remainder (Figure 6). Length data from the Japanese trawl fishery at Hancock during 1971-74 and 1976 are given in Table 6, and NMFS data for 1978-82 are plotted in Figure 15. Data from all seamounts combined and those from Hancock show a tendency toward slightly higher mean FL in the later years of the fishery compared with the earlier years. The FL ranges at all seamounts combined and for those at Hancock indicate the trawl fishery is harvesting a very narrow length range. Apparently the smaller and larger pelagic armorhead are relatively rare inhabitants of the seamounts since the trawls are capable of retaining much smaller fish. The largest known specimens from the seamounts area are a 495-mm total length (TL) female and a 498-mm TL male (Randall, 1980). The largest recorded pelagic armorhead is a 555-mm TL specimen from Cape Point, South Africa (Smith, 1964).

Annual mean FL by sex was derived from data collected at Hancock by NMFS during 1978-82. Females have a slightly larger mean FL than males. Table 7 gives the results of a two-way univariate ANOVA which indicated a highly significant difference in mean FL between the sexes and that the pattern of this difference is also highly significant in each year. Pooled NMFS and Japan Fisheries Agency (1974) sex ratio data for Hancock indicate no departure from a 1:1 ratio.

A parasitic copepod, _Pennella hawaiiensis_, on pelagic armorhead has been reported by Borets (1979). This ectoparasite is commonly found attached to the musculature of the dorsal region. The infestation rate of this parasite was 44 percent at Koko and 55 percent at Milwaukee. The Japan Fisheries Agency (1974) reported the frequent occurrence of small unidentified ectoparasites on pelagic armorhead taken at SE Hancock. Numerous small, unidentified parasites were found in this study on the gill filaments of virtually all pelagic armorhead. Intermuscular parasites were rare.

TABLE 5. COMBINED FORK LENGTH DATA OF PELAGIC ARMORHEAD TAKEN BY JAPANESE TRAWLERS AT SEAMOUNTS

Year	Sample Size	Mean (cm)	Range (cm)
1969	375	29.2	24-36
1970	166	29.2	26-34
1971	4,400	28.9	24-40
1972	6,410	27.4	20-34
1973	3,138	29.0	25-35
1974	20,724	28.8	21-37
1975	11,736	28.9	23-35
1976	8,517	29.5	15-35
1978	5,508	31.3	23-44
1979	2,412	30.9	21-39
1981	2,664	32.1	27-40

TABLE 6. FORK LENGTH DATA OF PELAGIC ARMORHEAD TAKEN AT HANCOCK SEAMOUNTS BY JAPANESE TRAWLERS

Year	Sample Size	Mean (cm)	Range (cm)
1971	1,199	28.8	25-34
1972	599	27.8	26-34
1973	200	28.7	27-33
1974	900	28.5	24-33
1976	93	28.8	27-31

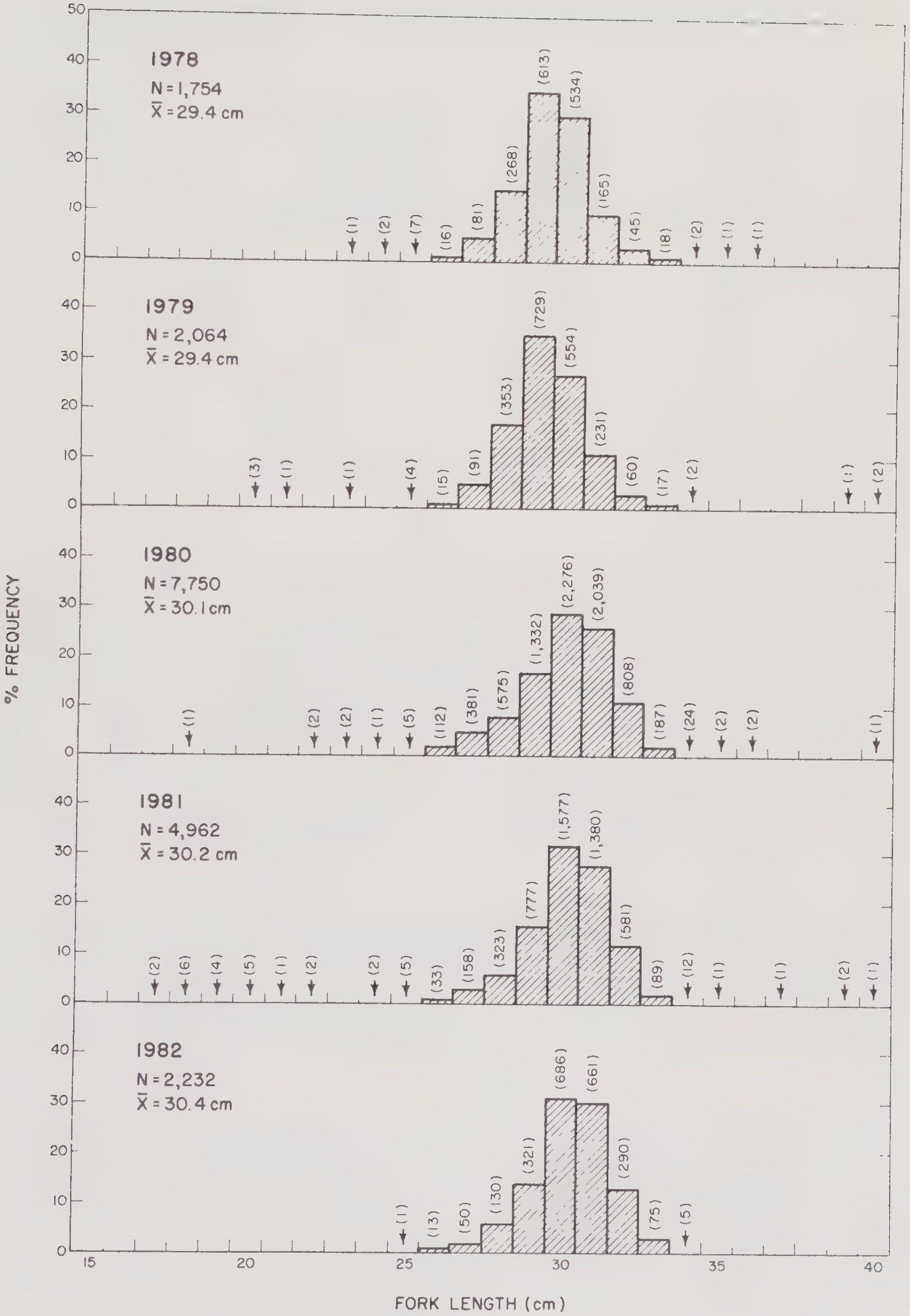

Figure 15. Yearly frequency distribution of pelagic armorhead at Hancock Seamounts from data collected by the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service. Values above bars represent the number of measurements within the interval.

TABLE 7. ANOVA ON LENGTH DATA, BY SEX, FOR PELAGIC ARMORHEAD TAKEN AT HANCOCK SEAMOUNTS BY JAPANESE TRAWLERS

Year	Number of Males	Mean Fork Length of Males (cm)	Number of Females	Mean Fork Length of Females (cm)	ANOVA		
					Source	d.f.	PR > F
1978	222	29.1	325	29.7	Sex	1	***
1979	461	29.0	577	29.7	Year	4	***
1980	2,302	29.7	1,759	30.5	Sex and Year	4	NS
1981	620	29.7	817	30.7			
1982	578	29.9	790	30.7			

Note: NS = $P > 0.05$; *** $P \leq 0.001$

Alfonsin

Alfonsin are primarily distributed within two areas of the Pacific northern hemisphere. Within the central North Pacific, alfonsin are found from Koko to Hancock within the Emperor-Hawaiian Ridge Area. In the western Pacific, an alfonsin fishery has existed for many years in Sagami Bay, Japan. Their distribution also extends south of Honshu, Japan to Izu, Kinansho, and further south to Komabashi Seamount near Palau (Chikuni, 1971; Sasaki, 1978). In the central North Pacific alfonsin are only found on seamounts, whereas in the western Pacific they are also found on continental shelf areas. Information on the worldwide distribution of alfonsin is given in Busaklin (1982).

Alfonsin apparently have a pelagic early life history; they subsequently adopt a demersal habit by age one. In the western Pacific, dispersal of eggs and larvae is strongly affected by the Kuroshio current. No information is available on eggs and larvae over the SE-NHR seamounts. Chikuni (1971) suggested that early life stages may be recruited between the two central areas, especially toward the SE-NHR seamounts.

In a tagging study conducted in Sagami Bay, most alfonsin were recaptured offshore. Alfonsin length-frequency data from several locations in the western Pacific indicate a pattern of increasing size with depth and a decreasing size with latitude. The length range of alfonsin in Sagami Bay (representing higher latitudes) was 17 to 20 cm compared with 35 to 50 cm from southern areas (Chikuni, 1971). Length-frequency data collected by NMFS in 1978-82 for Hancock are shown in Figure 16.

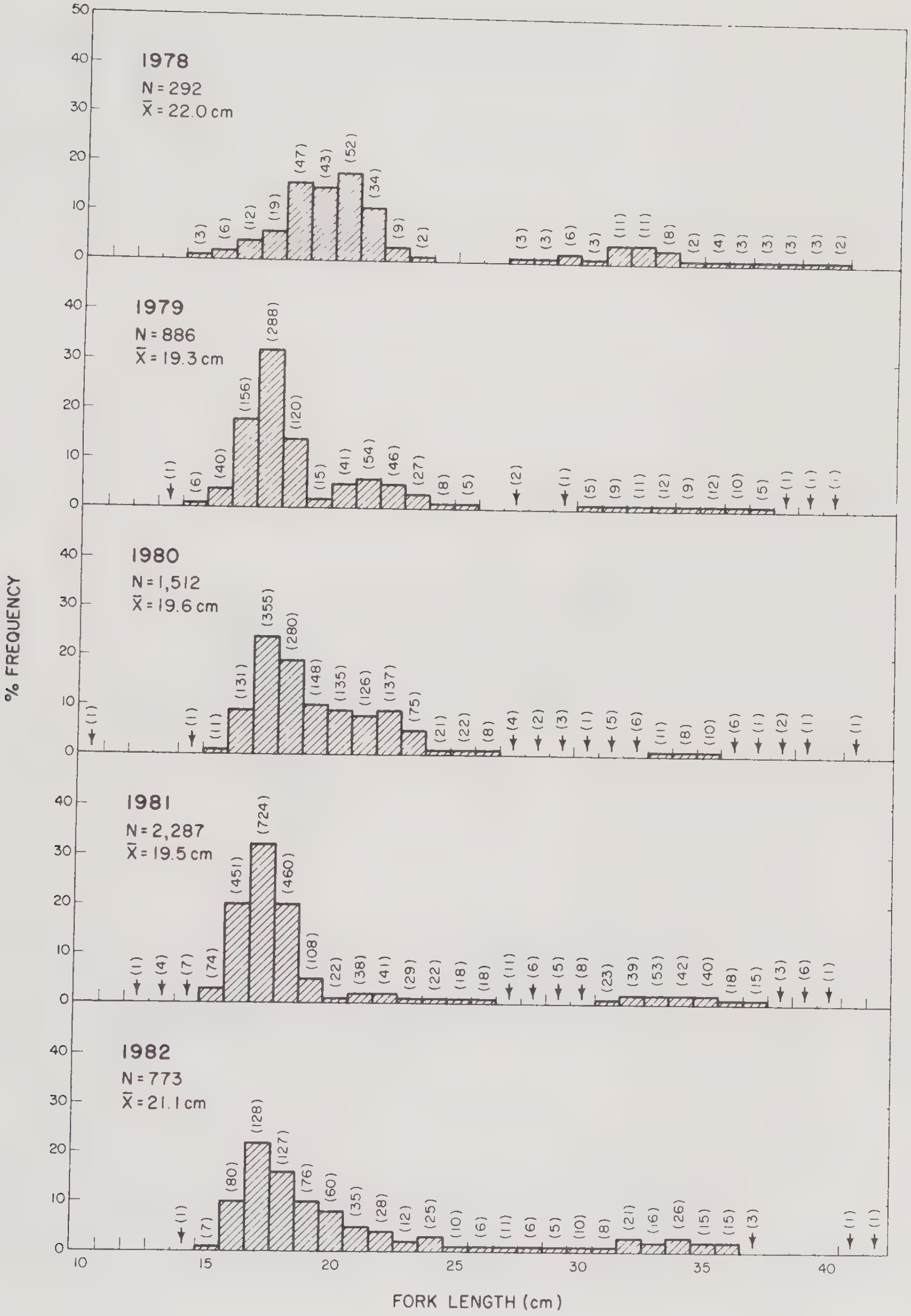

Figure 16. Yearly frequency distribution of alfonsin at Hancock Seamounts from data collected by the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service. Values above bars represent the number of measurements within the interval.

Although the smaller size group (similar to that from Sagami Bay) predominates, a larger size group is also sometimes present. The size distribution of alfonsin at Hancock apparently does not follow the distributional patterns reported for the western Pacific by Chikuni (1971). Figure 17 shows the distribution, by sex, of alfonsin from Hancock (NMFS data from 1978 to 1982). The distribution of the two sexes indicates that sexual dimorphism is not responsible for the existence of different size groups. Combined NMFS and Japan Fisheries Agency (1974) data show a nearly equal sex ratio at Hancock.

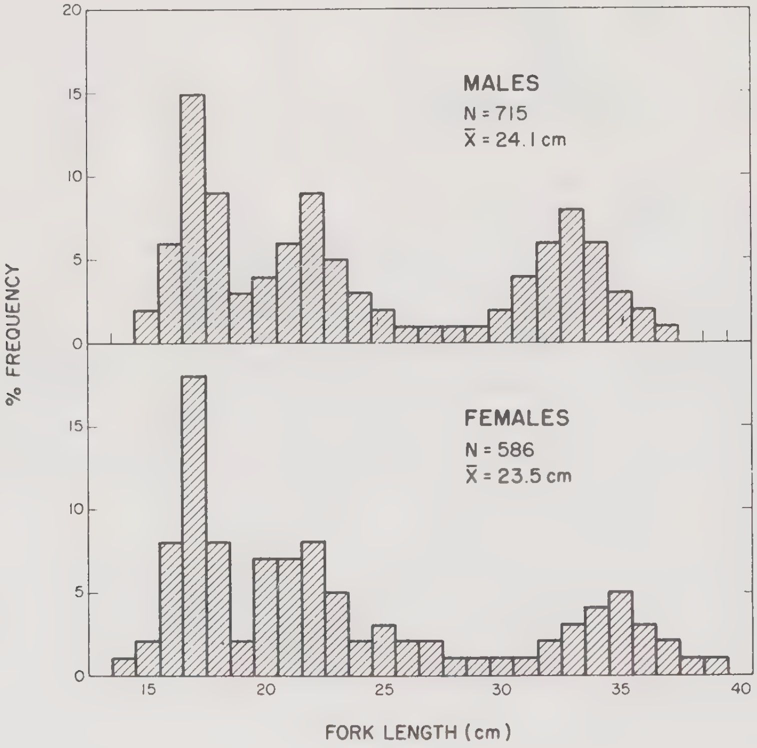

Figure 17. Frequency distribution for 1978-82 combined of alfonsin, by sex, at Hancock Seamounts from data collected by the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service

No information is available on spawning season (or the existence of reproductive alfonsin) at the SE-NHR seamounts.

U.S. foreign observers[7] have reported that many of the small, trawl-caught alfonsin appear sexually immature. Chikuni (1971) reported that in the western Pacific the spawning season is from August to October.

Based on a study of otoliths, Ikenouye (1969) determined the following age-length relationships for alfonsin:

Age	FL (cm)
1	9
2	19
3	26
4	30
5	33

These results suggest that the bulk of the alfonsin caught in the seamount trawl fishery are 2 years old (Figure 16). Ikenouye reported that alfonsin in the western Pacific first reach maturity by age three.

The feeding habits of alfonsin on the SE-NHR seamounts are not well known. Krill, mysids, copepods, myctophids, and other mesopelagic fishes have been found in alfonsin stomachs (Japan Fisheries Agency, 1974). Results of other Japanese survey cruises (Aomori Prefectural Fisheries Experimental Station, 1976) showed small fish to be the most abundant prey, followed by decapod and schizopod crustaceans. Barnett[8] identified prey items consisting of benthic shrimp, fish, and tunicates and also found relatively large amounts of fine silt in the gut.

MANAGEMENT

Japan is the only foreign nation thus far to fish under permit at Hancock since the establishment of the FCZ in 1977. Beginning in 1978, Japan was allocated half of a yearly total allowed level of foreign fishing (TALFF) of 2,000 MT (all species included). However, the Japanese have never attained the allotted quota. The total yearly Japanese catches at Hancock, determined by U.S. foreign observers[9] are as follows: 1978, 393.0 MT; 1979, 205.4 MT; 1980, 795.4 MT; 1981, 662.0 MT; and 1982, 393.0 MT.

The 1982 ex-vessel value (in U.S. dollars) was $763/MT (dressed) for pelagic armorhead and $240/MT (round) for alfonsin landed in Japan (R.T.B. Iversen, 1983: personal communication).

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[7] See footnote 1

[8] See footnote 1, specifically W.B. Barnett, 1982, Southwest Fisheries Center Administrative Report H-82-21.

[9] See footnote 1

No U.S. fishermen have yet fished commercially at Hancock.

Set forth in the preliminary management plan for the seamount groundfish fishery of the Pacific, as published in the Federal Register, U.S. management policy ideally requires the determination of a maximum sustainable yield (MSY). Given MSY it would then be possible along with other considerations, to calculate optimum yield. After assessing the level or potential level of harvesting by U.S. fishermen, a TALFF could then be derived.

Determination of MSY requires an accurate assessment of stock structure. Available biological information on pelagic armorhead indicates that one common stock exists among the seamounts of the SE-NHR. Hence, catch and effort data from all these seamounts could be incorporated in determining MSY. In this regard, the Japanese fishery data could serve as a basis for this determination. Also needed is an accurate delineation of the stock's home range. A determination of the home range requires a consideration of the distribution of pelagic armorhead by body type. All three body types have been found on the seamounts; however, only fat types inhabit the northeast Pacific during summer, their whereabouts after summer being unknown. Consequently, there is a question of whether the home range of the fat type extends well beyond the seamounts or whether the fat type represents an independent stock. Available biological information is still insufficient to conclude that the fat type represents a pelagic, predemersal phase and that ultimately these fish return to the seamounts. Until the status of the fat type is better understood, the determination of MSY based on seamount catches alone may be of little value for management purposes. Another management problem is the accessibility of this fishery to other fishing nations. Because most of the SE-NHR seamounts are located in international waters, there is some question as to how effectively the pelagic armorhead resources within the FCZ could be independently managed. The most effective management plan would ultimately adopt a holistic approach and thereby require the involvement and cooperation of all nations participating in this fishery.

SUMMARY

Until fairly recently, investigations of the SE-NHR seamounts were principally geological. With the Soviet discovery in 1967 of fishery resources on the seamounts, a series of biological and oceanographic studies began. Soviet oceanographic studies show the existence of intense vertical circulation and the meandering of surface currents near the seamounts. These physical processes are believed to be responsible for the higher plankton biomass found in this area compared with the more oligotrophic environment of surrounding waters.

The main fishing activity in this region has been the initiation of a trawl fishery on the SE-NHR seamounts. Of principal commercial importance is the pelagic armorhead and, to a lesser extent, alfonsin. During a 7-month period at the beginning of the fishery, the Soviets reportedly harvested 133,400 MT of pelagic armorhead. In 1969, the Japanese also entered the seamount trawl fishery. Annual Japanese catches for all seamounts combined ranged from 19,000 to 35,000 MT during 1972-76. However, catches sharply declined during 1977-81, ranging from 500 to 6,200 MT. With the establishment of the U.S. FCZ, the Hancock Seamounts came under U.S. jurisdiction and consequently various regulations were developed. Japan was the only foreign nation to fish under permit at Hancock during 1978-82. During this period, catches of pelagic armorhead were very low, reflecting a similar trend among the rest of the SE-NHR seamounts. No U.S. fishermen have fished in the seamount fishery. Other smaller scale fisheries operating on the SE-NHR seamounts were bottom longlining, primarily for alfonsin; bottom dragging for precious corals; and gill netting for squid and saury.

Surveys of Hawaiian Ridge seamounts south of Hancock revealed large differences in the ichthyofauna. The primarily deep water, benthic, and demersal fishes of the SE-NHR seamounts are replaced by subtropical reef and snapper-grouper fishes of the shallower southern seamounts. Seamounts 10-11, Ladd, and Nero appear to have a more transitional ichthyofauna.

Little is known about the life history of pelagic armorhead. Evidence indicates a common, reproductive stock on the SE-NHR seamounts. These fish apparently undergo diurnal vertical movements, becoming closely associated with the summits at night and the upper water column during daylight. Mesopelagic organisms appear to be an important food resource.

A still unresolved problem concerns the existence of three different morphological types among pelagic armorhead. The lean and intermediate type are brownish and predominate over the seamounts. The fat type has blue and white pelagic coloration, is infrequently caught over the seamounts and is the only type known to inhabit oceanic waters far from the seamounts. No meristic differences were found among the three types. Although the fat type is suspected to be representative of a pelagic, predemersal stage common to all members of this species, conclusive evidence is lacking. Resolving the status of the fat type in the population is needed before stock structure can be determined. Until then estimates of MSY must be based solely on seamount commercial catch data.

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The Propagation of Cod *Gadus morhua* L.

INFERENCES REGARDING PREDATION ON THE EARLY LIFE STAGES OF COD AND OTHER FISHES

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ABSTRACT

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Little information exists on the predation on the early life stages of marine fish in general and even less on cod. Thus the approach used in this review was to infer the predatory processes that may be significant in the early life history of cod using the general literature on the predators of marine fish eggs and larvae. The mortality of cod during the embryonic period is high indicating a high rate of predation and predation may continue to be the dominant source of mortality in later larval stages. The known predators of eggs and larvae are discussed as are intrinsic and extrinsic factors that affect vulnerability to predation. Recommendations are made for future research.

INTRODUCTION

The objective of this review was to characterize the process of predation on cod eggs and larvae in the sea. Little information exists on the predation on the early life stages of marine fish in general and even less on cod. Thus, the approach I have used in this review was to infer the predatory processes that may be significant in the early life history of cod using the general literature on the predators of marine fish eggs and larvae.

Predation, starvation, and certain abiotic effects (wave action, UV radiation, temperature and salinity changes) have been proposed as possible sources of the great mortality experienced by pelagic marine fish eggs and larvae in the sea. During the embryonic period (egg and yolk-sac stages) only abiotic effects and predation are sources of mortality because the embryo subsists on yolk. Abiotic effects occasionally may be important in the embryonic stages since these stages are the most susceptible to physical damage. Moribund eggs and larvae have been observed in plankton catches but these reports have been discounted in recent years and attributed to failure to wash plankton nets thoroughly between tows (May, 1974). Soleim's (1942) observation of a large number of dead or dying yolk-sac herring larvae, presumably killed by changes in temperature and salinity, appears to be an authentic case as the proper precautions were taken to avoid contamination from previous net hauls (Wiborg, 1976). Nevertheless, changes in temperature and salinity sufficient to kill large numbers of eggs or larvae in the open sea are probably rare, and experimental evidence indicates that other abiotic causes of mortality are unlikely. For example, pelagic eggs appear to be highly resistant to damage from wave action (Pommeranz, 1974) and significant damage from UV radiation seems to require sustained exposure for days in the upper 5 m of the water column, which seems unlikely in well mixed surface waters (Hunter et al., 1982). Thus the mortality during the embryonic period is good evidence for the existence of predation as a cause of natural mortality.

The mortality rates of embryonic marine fishes are often very high indicating high rates of predation. Mortality rates (z) of cod eggs from the North Sea range from 0.03 to 0.41 over 11 years and averaged about 0.25, implying a loss rate of about 22% per day (Daan, 1979, 1981). Considering the long incubation period of cod eggs (15-18 days at 5-7°C) these rates seem surprisingly high, being comparable to those of temperate northern anchovy which has only a 3 day incubation period (Table 1). Thus in the North Sea typically 98% of the cod eggs are probably consumed by predators before they hatch.

TABLE 1

Mortality rates of pelagic eggs and larvae in percent per day.

Fish	Year(s)	Stage	Mean	Range	Reference
Cod	1968-1977	Egg	22	3-33	Daan, 1976
Plaice	1947-1977	Egg	7	2-13	Harding et al., 1978
Plaice	1947-1971	Yolk-sac larvae	10	3-22	Harding et al., 1978
Anchovy	1980-1983	Egg	21	13-36	Unpub. data SWFC[1]
Anchoveta	1981	Egg	-	67	Santander et al., 1983
Sole	1969-1970	Egg	-	42-65	Riley, 1974

[1] Southwest Fisheries Center, La Jolla, California 92038, USA.

The range of mortality rates for cod eggs and for those of other species indicates that predation rates vary greatly from year to year, and such variation might account for the observed variations in recruitment, particularly if these predation rates persisted over subsequent life stages. Some evidence exists that the high predation rate encountered in the egg stage persists through the embryonic period, i.e., until the development of a functional eye and jaw and the onset of feeding. In plaice and northern anchovy the mortality rates of eggs do not differ much from that of yolk-sac larvae indicating no sharp transition in rates during the embryonic period (Harding et al., 1978; Hunter, 1982).

After the onset of feeding the argument for predation as the principle source of mortality is less compelling because starvation may also play an important role. All laboratory studies on pelagic fish larvae such as cod, herring, anchovy, and plaice (Hunter, 1981) indicate that they are highly vulnerable to starvation at the onset of feeding owing to their small size, short sighting distance for prey, slow cruising speeds during the search for food, low capture success, and high food density requirements. On the other hand, new studies in large semi-natural enclosures seem to indicate that predation is the major source of mortality in the sea. In such enclosures, 3-10% of cod larvae survived through metamorphosis at food densities equivalent to those encountered in the sea (Ellertsen et al., 1981). Since these survival rates are much greater than those of larvae in the sea, the absence of predators in the enclosure appears to be the reason for the remarkably high survival.

New tools now exist which can be used to determine if the apparent vulnerability to starvation inferred from laboratory work translates into a high rate of natural mortality. In fact, identification of starvation as a cause of mortality in the sea is now easier to assess quantitatively than the effects of predation, because starving larvae can now be accurately identified using histological criteria (Theilacker, 1978; O'Connell, 1980), and slow growth of larvae can be detected using daily increments on larval otoliths (Methot and Kramer, 1979). Such measurements hold the key to determining the relative importance of starvation and predation (by the difference between starvation mortality and total mortality) during the post-embryonic phase of larval life. Sea studies using these new techniques are just beginning (no data exist on cod) but present evidence indicates predation plays the dominant role in larval mortality (O'Connell, 1980; Methot and Kramer 1979).

These lines of evidence seems to indicate that predation during the embryonic period is high and variable, and it probably remains the principle source of mortality throughout the rest of the early life history of cod. The latter conclusion is of course speculation, although the results of the enclosure studies seem quite convincing in this regard. Proof will await assessment of the rates of starvation in the sea.

KINDS OF PREDATORS

Crustacea and chaetognaths

Consumption of marine fish larvae by copepods, euphausiid shrimp, hyperiid amphipods and chaetognaths has been studied in small (0.2-3.5 litre) containers in the laboratory. For example, in the California Current region, 11 species of calanoid copepods, and euphausiid shrimp were capable of capturing or fatally injuring yolk-sac anchovy larvae (Lillelund and Lasker, 1971; Theilacker and Lasker, 1974), and to the north in Dabob Bay, Washington, the calanoid *Euchaeta elongata* and several species of crab larvae have been identified as predators of yolk-sac hake larvae (Bailey and Yen, 1983). Additional species of calanoids observed preying on larvae are mentioned by Lebour (1925). Laboratory studies seem to show that small carnivorous arthropods (calanoid copepods, amphipods and euphausiids) can attack and kill significant numbers of marine yolk-sac fish larvae if the concentrations of larvae are suitably high (Table 2). Consumption of fish larvae by chaetognaths has been frequently inferred from examination of preserved specimens taken in plankton tows (Lebour 1922, 1923; Alvariño 1980). On the other hand, laboratory experiments on two species (*Sagitta elegans* and *S. setosa*) seem to indicate that they are not important predators. *Sagitta* required a 24h starvation period before consuming any larval fish, they strongly preferred copepods to larvae, and they ate only first feeding larvae, as younger larvae (yolk-sac) and older ones were not eaten (Kuhlmann, 1977). Clearly, more information is needed on larval predation by chaetognaths.

Few of the small invertebrate predators studied to date seem to be effective predators of pelagic fish eggs. Laboratory tests indicate that neither *Euphausia* (Lillelund and Lasker, 1971; Bailey and Yen, 1983), *Sagitta* (Kuhlmann, 1977) nor crab larvae (*Parathemisto* and others) and shrimp larvae, (Bailey and Yen, 1983) are significant predators of pelagic fish eggs. Presently, the only pelagic crustacean identified as a predator of pelagic eggs is the amphipod *Calliopius* (Bailey and Yen, 1983), but very few of the vast number of pelagic crustacea have been considered.

Only the yolk-sac stage of marine fish larvae appears to be vulnerable to these small carnivorous arthropods. These predators appear not to be able to consume significant numbers of pelagic eggs and the number of fish larvae attacked drops rapidly at the end of the yolk-sac period. For example, the number of yolk-sac anchovy larvae killed by *Labidocera* females declined from 16 newly hatched anchovy

Table 2. Results of various laboratory studies on the predators of marine fish larvae.

Predator species	Prey species	Relative life stage vulnerability[a]			Maximum attack rate		Minimum prey density and attack rate		Natural incidences of predation	Projected effects	References
		egg	yolk-sac	first feeding	prey density n/ℓ	prey attacked per day	density n/ℓ	attacks per day	% stomachs with prey		
Copepods											
Labidocera jollae	anchovy	0	1	0.6	8.6	18[b]	1.4	5[b]	---	---	Lillelund & Lasker, 1971
Labidocera trispinosa	anchovy	0	1	0.4	4.2	5[b]	1.4	1[b]	---	---	Lillelund & Lasker, 1971
Euchaeta elongata	hake	0	1	0.2	10-25	2[b]	2.0	0.5[b]	31-43	---	Bailey & Yen, 1983
Euphasiid shrimps											
Euphausia pacifica	anchovy	"low"	1	0.2	11-14	10[c]	5-6	6[c]	---	Able to consume 2,847 larvae/d/m^2 (in excess of actual larval density in sea)	Theilacker & Lasker, 1974
Amphipods											
Hyperoche medusarum	herring	---	X	---	100	11	10	2.4	24-58	---	Westernhagen & Rosenthal, 1976; Westernhagen, 1976
Chaetognaths											
Sagitta setosa *S. elegans*	sprat, anchovy	0	0	1.0[d]	N.E.[e]	N.E.[e]	7.5	1.5	---	---	Kuhlmann, 1977
Jellyfish											
Aurelia aurita (12-14 mm dia)	herring	---	X	---	9	7/hour[f]	0.5	1/hour[f]	9-40[g]	Accounts for 4.4% of larvae per day	Möller, 1980 Bailey & Batty, 1983
Fish											
Engraulis mordax	anchovy	X	---	---	10	17,000	1	500	42	Accounts for 32% of the natural mortality of eggs	Hunter & Kimbrell, 1980b Hunter & Dorr, 1982
Clupea harengus pallasi	herring	---	X	---	---	14,000	---	2,000	---	Co-occurrence of herring larvae with adults is rare	Hourston et al., 1981

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[a] 1 = maximum vulnerability, other numerical values are relative to maximum; X = only the indicated life stage was examined.

[b] Number attacked decreased when alternate prey present.

[c] Number attacked unaffected by presence of alternate prey.

[d] Larvae older than 4 days escaped.

[e] Density had no effect (= N.E.) between 7.5 - 150 larvae/ .

[f] Hourly rates given because medusae began to satiate after ingesting 5-6 larvae.

[g] 6-50 mm dia. jellyfish.

larvae per day to about 7 per day for 168-h-old larvae.

The presence of an alternative prey (copepods) depresses the rate of larval predation in the carnivorous copepods (Lillelund and Lasker, 1971; Bailey and Yen, 1983) but apparently not in euphausiid shrimps. For example, at equal densities of *Pseudocalanus* and hake larvae the presence of *Pseudocalanus* depressed the predation rate of *Euchaeta* on hake larvae by 60% (Bailey and Yen, 1983). Since copepods, rather than larval fish dominate most plankton assemblages, this is an important effect. The predation rates observed in the laboratory probably are seldom realized in the sea because the larval fish densities are much lower in the sea and more numerous alternative prey exist for the predators. Yolk-sac herring are a possible exception as they appear to achieve remarkably high densities in the sea (20 larvae/litre at the surface; Westernhagen and Rosenthal, 1976).

Field evidence also indicates that, hyperiid amphipods and carnivorous calanoid copepods consume significant numbers of fish larvae although specific identification of remains of larvae in the stomachs is uncertain. Hyperiid amphipods co-occur with yolk-sac herring larvae for 40 days in Departure Bay, British Columbia, and remains of fish larvae are the most abundant item in their guts (Westernhagen and Rosenthal, 1976; Westernhagen, 1976). Fish larvae, especially herring and *Ammodytes*, make up 23% of the food of the hyperiid amphipod *Parathemisto gaudichaudi* during April and June in the North Sea (Sheader and Evans, 1975). Fish larvae (presumably yolk-sac stages of hake) occurred in 30 to 43% of the *Euchaeta* stomachs examined by Bailey and Yen (1983).

Field evidence from freshwater lakes indicates that marine cyclopoid copepods might be as important predators as the predacious calanoids. Adult female freshwater lake cyclopoid copepods (*Diacyclops thomasi* and *Acanthocyclops vernalis*) are reported to feed on alewife (*Alosa* *pseudoharengus*) larvae; 1-4% of alewife larvae (typically 3-5 mm) taken in plankton tows had attached cyclopoid copepods; and all were taken at night, indicating that the larvae may be more vulnerable when less active (Hartig et al., 1982). Similarly, Brewer et al., (1983) found the cyclopoid copepod (*Corycaeus anglicus*) attached to 5% of white croaker larvae (*Genyonemus lineatus*) taken in net tows from nearshore waters of Southern California. Only small larvae were susceptible to capture as 93% of the larvae with attached copepods were less than 4 mm long. It is possible that the predation observed in these reports occurred in the plankton net. Nevertheless, it seems important to evaluate the predatory potential of marine cyclopoids because of their great abundance. For example, cyclopoid copepods constitute 20-30% of the total copepods occurring in Norwegian coastal plankton (Wiborg, 1954).

Predation by Jellyfish and Ctenophores

Laboratory and field observations over the years have identified at least 34 species of medusae and about 5 species of ctenophores as predators of the eggs and larvae of marine fishes. This probably represents a small fraction of potential predators given the hundreds of species and their carnivorous feeding habits. These records are based largely on casual observation in the laboratory or food habit studies of sea caught individuals where fish eggs and larvae are typically an incidental part of a zooplankton diet. Thus, it seems pointless to list all species and references here, but the majority are mentioned in various reviews or surveys (Lebour, 1922, 1923, 1925; Fraser, 1969; Bieri, 1961, 1970; Larson, 1976; Möller, 1980; Ari and Hay, 1982) and additional references are mentioned in the context of this review.

Consumption rates of fish larvae by large medusae and ctenophores at times can be very high. Fraser (1969), in his review, speculates that a lifetime consumption of 50-250 larval fish by each hydromedusa, about 450-500 by each *Aurelia*, and about 15,000 by each *Cyanea* is probable. Stevenson (1962) commented that as many as 45% of the Pacific herring larvae taken in a sample had been or were being devoured by ctenophores (*Pleurobrachia* spp.) on one occasion in 1947, but he continues that predation by ctenophores is generally not a serious source of mortality; in almost 4,000 plankton samples containing larval Pacific herring, evidence of such a mortality occurred in fewer than 100 samples. In a shallow cove in the Gulf of California, the siphonophore *Rhizophysa eysenhardti* was estimated to consume about 8.8 fish larvae per siphonophore per day which may have represented about 26% of the various species of fish larvae present in the cove (Purcell, 1981). Major blooms of this species in the Gulf are probably sporadic, however.

The best documented example of predation by jellyfish on fish larvae is for the scyphomedusa *Aurelia aurita* which appears to be an important predator of yolk-sac herring larvae. In Kiel Fjord (western Baltic) consumption rates of *Aurelia* averaged about four larvae per medusa per day during May, indicating that at least 2-5% of the total stock of yolk-sac herring larvae are eaten per day (Möller, 1980). No correlation existed between the size of the medusa and the percentage of medusae containing larvae but the number of larvae per medusa increased with increasing medusa diameter from up to 10 larvae in 12 mm medusae to 68 larvae in 42 mm medusae. Laboratory work indicates that *Aurelia* (12-14 mm) have the capacity to kill herring larvae at rates up to 7/h with satiation occurring after consumption of 5-6 larvae (Bailey and Batty, 1983). These authors also point out that both efficiency of capture and encounter rates increase greatly with medusa size, corroborating Möller's field observations. The evidence for this species and perhaps other large jellyfish being a major predator of cod larvae is not strong. *Aurelia*, and other large jellyfish are most abundant during the summer, whereas peak months of spawning of cod are February and March (at least in the Baltic; Möller, 1979). On the other hand, the ephyrae stage might be important because they become abundant in March (Möller 1979) and ephyrae of *Aurelia* only a few days old will eat larval fishes (Lebour, 1922).

The size-specific vulnerability of cod and other fish larvae to jellyfish is essential for estimating overall impact on the population and interpreting mortality rates, yet little data exist other than for the yolk-sac stages. The vulnerability of cod must decline greatly over the larval stages since late larval and pelagic juvenile cod are known to accompany and seek shelter beneath large jellyfish (*Cyanea capillata, Aurelia aurita, Rhizostoma pulmo*) as do many other gadoid fishes (Ward, 1912; Mansueti, 1963). Young whiting, *Gadus merlangus*, which show the same behaviour appear to have developed a certain degree of immunity from the discharge of nematocysts of *Cyanea* and presumably cod are similarly immune (Dahl, 1961). Thus these large jellyfish seem unlikely predators of older cod larvae and juveniles.

Consumption of pelagic fish eggs by jellyfish and ctenophores seems to be mentioned much less frequently in the literature than predation on larvae. About five species of medusae (Lebour, 1922, 1923; Phillips et al., 1969; Bailey and Yen, 1983), two chondrophora (Bieri, 1961, 1970), and two ctenophores, *Pleurobrachia* (Lebour, 1922, 1923; Bailey and Yen, 1983) and *Mnemyopsis leidyi* (Burrell and Engel, 1976), have been reported to consume pelagic fish eggs as well as larvae. *Pleurobrachia* might be a significant predator of cod eggs and early larvae as it reaches peak abundance in January-February in the Baltic, which corresponds to peak production of cod larvae (Möller, 1979). At filtering rates that range from 5 ml/day for animals less than 0.8 mm to 1,150 ml/day for 7.2-8.3 mm animals (Reeve and Walter, 1976), dense swarms of *Pleurobrachia* certainly would have the capacity for removing significant quantities of eggs and yolk-sac larvae. Eggs and larvae that concentrate at the sea surface are probably highly vulnerable to the neustonic jellyfish *Velella* and *Porpita* (Chondrophorae) (Bieri, 1961, 1970). Off the coast of California in May, fish eggs (*Trachurus symmetricus*) were the most important and common food item (48% of prey) of *Velella* (Bieri, 1961).

The occurrence of swarms of ctenophores or jellyfish appears to be very episodic. Ctenophore populations, for example, appear to be capable of very rapid growth resulting in the sudden appearance of dense swarms. Reeve and Walter (1976) conclude from studies of growth of *Pleurobrachia* in large bags (68 m^3) that populations are capable of increasing by more than 50% per day. Although patches or swarms of ctenophores and jellyfish are known to occur in the open sea, the most frequent reports are from inshore and often partially enclosed areas such as bays, fjords and estuaries. Burrell and Engel (1976) mention that concentrations of ctenophores seem to be short lived in neritic or oceanic water but they may persist for months in confined areas such as estuaries. Thus, significant predation by jellyfish and ctenophores may only occur on the occasions when spawning and outbursts of jellyfish occur together; the probability of such events seems to be greater in partially enclosed areas than in the open sea. An inverse relationship between *Aurelia* and larval herring abundances in Kiel Fjord clearly illustrates this point, as the highest larval abundances occurred in years in which significant numbers of herring had hatched before the annual outburst of *Aurelia* (Möller, 1982). These inverse correlations between jellyfish or ctenophore abundance and larval abundance are relatively common (Alvariño, 1980), but only in herring is it good evidence for consumption by the medusae, since herring have geographically fixed spawning grounds and the parents can not move elsewhere to avoid concentrations of medusae. On the other hand, low abundance of eggs and larvae of pelagic spawners could also be attributed to avoidance of such regions by the parents. This seems likely for planktivorous fishes since the zooplankton foods of these fishes are consumed by medusae and ctenophores, and spawning schools may not remain long in areas where forage is low.

Other invertebrates

Marine polychaetes and squid undoubtably consume marine fish larvae but little is known regarding their importance in larval mortality. Lebour (1923) mentions that the polychaete *Tomopteris helgolandica* consumes herring, and other fish larvae and squid are known piscivores. Owing to their size, agility, and piscivorous habits, they are capable of feeding on many life stages of fishes, not just the youngest larval stages, as is the case for most invertebrate predators. Newly hatched squid (*Loligo opalescens*) prefer fish larvae to brine shrimp adults, and the daily ration of a newly hatched individual is equivalent to 14 yolk-sac anchovy per day, and at 8 mm their daily ration is 135 anchovy larvae (Hurley, 1976).

Fishes

Ample evidence exists that pelagic planktivorous fishes consume pelagic eggs and larvae. In the southern North Sea cod eggs are consumed by herring, sprat, and stickleback. The highest mean rates were 5-6 cod eggs per sprat or herring with the eggs of plaice and other species being consumed in considerable quantities as well (Daan, 1976). Cod eggs were more abundant in the plankton than plaice but herring and sprat seemed to consume more plaice eggs. This might be related to the fact that plaice have larger eggs or possibly that the eggs of plaice were more concentrated than those of cod. Daan's study also identified herring as a major consumer of fish larvae, as herring larvae comprised 10-60% of the weight of the stomach contents of herring in some of the collections.

That herring and other planktivorous fishes are major consumers of fish eggs and larvae is also indicated by a number of other studies. For example, 54% of the stomach contents of herring and 45% of sprat were composed of fish eggs and larvae in the southern North Sea (Pommeranz, 1981), and in southern New England waters and Georges Bank, eggs and larvae of fishes represented 4.5% of the Atlantic mackerel diet by weight and 0.4% of that of herring (Maurer, 1976). Similarly, 83% of the prey consumed by Atlantic mackerel larvae (13-19 mm) were other mackerel larvae. Cannibalism probably occurred at night during an upward migration of the larger larvae as they passed through layers where smaller individuals were abundant (Grave, 1981). Pacific mackerel larvae, *Scomber japonicus*, are also larval fish predators (Hunter and Kimbrell, 1980a). Along the Peruvian coast, fish larvae and appendicularians were the principal foods of Pacific mackerel larvae, with sardine and Pacific mackerel larvae occurring in larval mackerel stomachs; larvae as small as 3.7 mm were piscivorous (Lipskaya, 1982). Young pelagic stages of cod co-occur with Atlantic mackerel in the North Sea (Jones, 1983); consequently nearly all life stages of mackerel can be considered as potential predators of cod larvae. Harding et al. (1978) examined the stomach contents of fish predators taken in egg patches in the southern North Sea. Sixty-two percent of the prey items in the stomachs of herring, and 96% of those in the stomachs of anchovy (*Engraulis encrasicholus*) were fish eggs or larvae, whereas other potential predators, *Merlangius merlangus*, *Melanogrammus aeglefinus*, *Limanda limanda*, *Eutrigla gurnardus*, and *Sprattus sprattus* contained only a few fish eggs or larvae.

Capelin are also indicated as possible consumers of cod eggs and larvae since cod eggs, as well as other fish eggs and larvae have been identified in their stomachs (Pozdnyakov, 1961).

Cod larvae and pelagic juveniles are likely predators of larval cod. Laurence et al. (1981) inferred that cannibalism occurred in cod rearing tanks because variability in length declined and survival decreased in groups of cod larvae maintained at low food densities. Variability in length increased until an age of one month after which it decreased in direct proportion to the density of prey in the container, indicating the existence of cannibalism. Ellertsen et al. (1981) also suggests that cannibalism occurred in their enclosure study because the survival of a group of cod larvae reared with older, near metamorphic individuals, was much lower than expected.

This discussion indicates that planktivorous fishes such as herring, sprat, pilchard, mackerel and others consume eggs and larvae of cod and other marine fishes. This could be expected since pelagic fish eggs and larvae differ little in size and avoidance capabilities from the typical foods consumed by such fishes, and if encountered they would be consumed along with their typical foods (copepods and euphausiids).

Pelagic planktivorous fishes can be abundant in cod spawning habitats and therefore could be responsible for a significant proportion of the mortality of cod eggs and larvae as well as that of other species. For example, Edwards and Bowman (1979) list 16 important species of pelagic planktivorous fishes from a cod habitat in the western Atlantic (continental shelf off New Jersey and Nova Scotia) without even considering the pelagic planktivorous life stages of the demersal fishes in that area. They estimated the zooplankton consumed by the two most abundant planktivorous species (Atlantic herring and Atlantic mackerel) varied from $2 \cdot 10^6$ to $26 \cdot 10^6$ tons annually for herring and from 4 · 10^6 to 28 · 10^6 tons for mackerel depending on their population sizes. Clearly, fluctuations in the size of these two major planktivorous fish stocks might induce major variation in the mortality of cod eggs and larvae even if cod early life stages were an incidental part of their diet. This suggests that a direct causal relationship might be responsible for the observed antagonistic behaviour of pelagic stocks (herring and sprat) and demersal stocks (cod and plaice) in the North Sea (Daan, 1976).

The proportion of egg and larval mortality that can be attributed to predation by planktivorous fishes has rarely been determined for any species. Daan (MS presented at the ICES council meeting in 1983) estimates that at least 1% of the eggs produced by cod and at least 7% of those produced by plaice are consumed by herring. This may be an underestimate because he assumed the digestion time for an egg was one day and because the herring stock in the North Sea is still at a rather low level. The only published study where cannibalism or predation has been related to natural mortality is that of Hunter and Kimbrell (1980b). They estimated that northern anchovy stomachs contained a mean of 5.1 anchovy eggs/stomach and using an instantaneous coefficient of gastric evacuation of 0.71/h they estimated the daily consumption of eggs to be 85.8 eggs/fish or about 17% of the daily egg production. MacCall (1980), using a new estimate of natural mortality of eggs (Z = 0.39) and a few other modifications, estimated from their data that cannibalism on eggs could account for 28% of total egg mortality.

Hunter and Kimbrell (1980b) noted that the eggs were eaten by filtering, but this process appears to be non-random, since consumption of eggs in the sea increased as the 1.6 power of egg abundance although the form of the relationship is unclear. At times anchovy schools probably aggregate on patches of eggs rather than taking them incidentally when feeding on other zooplankton, because egg densities in the sea are at times high enough to stimulate selective filtration (Hunter and Dorr, 1982).

VARIATION IN VULNERABILITY

The vulnerability of a larva to its predators is controlled by the intrinsic characteristics of size and maturational state, and by various extrinsic variables including larval forage, temperature, alternative prey for the predator, and visibility.

Intrinsic factors

The most important factor affecting vulnerability of larvae to predation is without a doubt the maturational state. The least mature stages (egg and yolk-sac) are also the most defenceless, suffer the highest losses, and are vulnerable to the greatest variety of predators ranging from small invertebrates to fishes. I know of only two studies in which the decline in vulnerability to predation with larval maturation has been directly studied, although the marked decline in the capture success of plankton nets with larval size is an important source of indirect evidence (Smith and Richardson, 1977; Hunter, 1981). In her thesis work, L. Dowd (University of Miami, personal communication, 1983) finds that the consumption rates of juvenile bay anchovy (*Anchoa mitchilli*) decline exponentially from about 80 sea bream larvae per hour (*Archosargus rhomboidalis*) for 2.5 mm larvae to about 10/h for 4.5 mm larvae. She found that the yolk-sac stages and eggs were less vulnerable than 2.5 mm larvae because lower activity levels made the yolk-sac larvae less visible. Webb (1981) provided a study on changes in vulnerability of northern anchovy to capture by the aquarium fish *Amphiprion percula*. The success of anchovy in avoiding capture increased linearly with size, with the percentage of larvae that responded to attack increasing from 9% in yolk-sac larva to 85% in 12 mm larvae.

The improvement in the avoidance of predators with maturation may be due to decreases in the latency of the escape response, increases in the speed and stamina of avoidance movements or some combination of these factors. Webb (1981) found that the critical element in the enhanced ability of longer larvae to escape the predator was the latency of the startle response, as only larvae that responded too late or not at all were caught. Thus the maturation of sensory systems seems to be more important than an increase in burst speed for this particular predator.

The mode of attack of a predator determines which factors are of greatest importance in avoiding capture. For example, the striking behaviour of fishes range over a continuum from sustained pursuit to sudden lunges (Webb and Skadsen, 1980). Lungers usually start an attack with the body position in an "S" shape, strike at the prey at high speed from short range and seldom pursue the prey if the attack fails, whereas pursuers start with the body positioned in a "C" shape, strike at slower speed from greater distances, and persistently chase the prey if the first attempt fails (Webb and Skadsen, 1980; Webb, 1983; Webb, Univ. of Mich., personal communication, 1983). Clearly maturation of sensory systems will be of utmost importance in avoiding the attack of lunging predators, whereas both locomotor and sensory systems are important in avoiding pursuing predators.

Extrinsic factors

Two of the most important extrinsic factors that affect vulnerability to predation are temperature and the abundance of larval forage. Low temperature or lack of food slows growth and thereby increases the duration that larvae remain in the smaller and most vulnerable life stages. Poor year-classes of Pacific sardine were associated with cold water temperatures and high food abundance, and it may have been the prolongation of the larval phase by low temperature resulting in higher predation that led to weak year-classes (Murphy, 1961). In support of this argument Murphy calculated that a 3° decline in water temperature (17-14° C) could decrease by 10 fold the number of sardine larvae that attain 21 mm. Prolongation of the early life stages of cod by low temperature might also increase mortality rates as a 3° decline in temperature (10-7° C) increases the time from fertilization to metamorphosis by about 20% (Laurence and Roger, 1976; Laurence, 1978).

An increase in vulnerability to predators as a result of slow growth can be caused by low food abundance as well as by temperature. Dowd (University of Miami, personal communication, 1983) found that sea bream larvae reared on low food rations were much more vulnerable to predation by juvenile bay anchovy than were those reared on a higher ration. She demonstrates that the increase in vulnerability can be explained entirely by the smaller size of larvae fed the lower ration. Lack of food may also increase vulnerability because of a deterioration of escape response of starved larvae. Twice as many hake larvae were attacked by the carnivorous copepod *Euchaeta* when they were starved for 3-4 days than when not starved (Bailey and Yen, 1983). As the larvae differed little in size the increased vulnerability may be attributed to a degenerated escape response.

Other extrinsic factors such as presence of alternative prey, abundance of predators, and patchiness of eggs and larvae were mentioned previously. I will not dwell on these factors here other than to point out that the presence of alternative prey consistently reduces predation rates in most laboratory studies to date. Other factors which have yet to be studied in larval fishes are the effect of the onset of schooling, shelter-seeking beneath jellyfish, effects of vertical movements or currents which may concentrate eggs or larvae, visibility of predators and prey at different times of day and in different water types, and temperature-specific activity levels of larvae, any of which may alter the attractiveness of larvae for certain predators.

DISCUSSION

All the well documented accounts for consumption of eggs and larvae by invertebrate predators and most of those for fish, are for species other than cod; the clupeoids, anchovies and herring comprise the majority of such records. Owing to the similarity in size of pelagic eggs and larvae, it seems likely that cod larvae at the same life stage would be vulnerable to the predators discussed in the previous sections if cod larvae co-occurred with them. Two undocumented accounts seem to support this view; Lee (1966) mentions that the amphipods *Parathemisto libellula* and *Pseudolibrotus* sp. consume cod larvae, and it is noted in Fraser (1962) that *Pleurobrachia* also feed on cod larvae.

The well documented high mortality of cod eggs is certainly the best evidence for a high rate of predation during cod early life history, yet, the identity of the predators primarily responsible for these losses still remains in doubt. The planktivorous fishes, sprat, herring and others consume cod eggs but on the basis of present evidence it seems unlikely that they can account for all the losses. Certainly, medusae and ctenophores (particularly *Pleurobrachia*) may consume significant quantities of cod eggs. The identification of the major predators of cod eggs is not a trivial question since cod exist as eggs for about 20% of the period between fertilization and metamorphosis. In addition, consumers of eggs (the planktivorous fishes and ctenophores) are also likely to be important consumers of yolk-sac stages as well, but yolk-sac stages are less commonly detected because of fast digestion rates (see next section). In fact, mortality rates of anchovy (Hunter, 1982) and plaice (Harding et al., 1978) often do not differ much between egg and yolk-sac stages, indicating that eggs and yolk-sac stages may be vulnerable to the same predators.

The taxa of predators that may be the most important in the early life history of cod at any life stage are unknown. The literature I have discussed for other species of fishes indicates that the small crustaceans (copepods, euphausids and amphipods) are important consumers of only the yolk-sac stages, whereas planktivorous fishes consume eggs, yolk-sac stage and older larvae as well. The larger invertebrates (ctenophores, squid, and some of the medusae) are also certainly able to consume larger larvae as well. The consumption rates of fishes increase much more with an increase in egg or larval density than do consumption rates of the smaller invertebrates. Herring or sprat would be capable of consuming thousands of cod eggs or yolk-sac larvae per day if the density were sufficiently high, whereas the smaller invertebrates satiate rapidly and maximum attack rates are only 2-6 larvae per day. This is an important distinction because it indicates that predation by fishes is more likely to have a stronger dependence on prey density than predation by small invertebrates. It seems appropriate, owing to the lack of information on predation and the inherent difficulty of such studies, to conclude this review with a discussion of the problems inherent in investigations of the predators of marine fish eggs and larvae.

Problems in estimating effects of predators

Accurate estimation of the effect of pelagic predators on the success of year-classes of fishes is perhaps the most difficult of all research on recruitment processes. Some of the major difficulties in a quantitative assessment of predation on eggs and larvae are: the incidental nature of eggs and larvae in the diets of their predators, which requires an assessment of the role of alternative prey; the patchiness of the youngest stages (egg and yolk-sac stages) and the rarity of the older stages in the plankton; the rapid digestion of early eggs and early larvae in the stomach of predators; biases resulting from predators feeding within net catches, and from undersampling large jellyfish and ctenophores; and, of course, the great diversity of potential predators. I discuss some of these issues below and suggest some approaches.

It has long been recognized that abnormal feeding may occur among raptorial copepods, amphipods, and chaetonaths in the crowded conditions of plankton samples. Many of the food habit studies may yield unnaturally high predation rates on larvae because chance encounters are greatly increased. Records of feeding on larvae by chaetonaths might fall in this category because laboratory work does not seem to identify them as important larval predators (Kuhlmann, 1977). Insertion of dyed larvae within the net prior to a tow might be a method of correcting for this posible bias as this technique has been successfully used in stomach analyses of trawl caught fishes (Lancraft and Robinson, 1979; Robinson and Bailey, 1982).

The rapid digestion of yolk-sac larvae by jellyfish and fishes, and their total destruction by crustacean predators greatly reduces the chance of detection of predation. Within 5 hours, yolk-sac herring larvae are digested beyond recognition by *Aurelia* at 10-12°C (Möller, 1980), and digestion of the smaller yolk-sac larvae of pelagic spawners proceeds much more rapidly. Larvae of American flounder and *Gadus saida* are totally digested except the eyes in 1.5 hours in *Aurelia* stomachs and take only 2 hours to disappear completely (Fraser, 1969). Similarly, the yolk-sac to first feeding stages of northern anchovy are digested beyond recognition in the stomachs of adult anchovy in 0.5 hours at 16°C (Hunter and Kimbrell, 1980b). Eggs in anchovy stomachs disappear at a rate of about 50%/h; eggs are detectable somewhat longer than yolk-sac anchovy larvae, presumably because the chorion is more resistant to digestion than is the larva. The rapid digestion of eggs and early larvae has two important implications. Low average numbers in the stomachs of predators may indicate a much greater impact than anticipated because the daily ration increases markedly when adjusted by a rapid gastric evacuation rate (Hunter and Kimbrell, 1980b). Secondly, net tows or trawls should be of short duration since typical duration of trawl hauls may exceed the duration of detectability of yolk-sac stages. To my knowledge no one has examined the change in the rate of digestion of larvae in predator stomachs as a function of larval size, although it is clear that older larvae may remain in the stomach for much longer periods than yolk-sac stages. Ironically, the most abundant stages which have the highest probability of occurring in predator stomachs, disappear from those stomachs at the highest rate, whereas larger larvae which are presumably more resistant to digestion may be so rare that quantitive assessment through stomach examination may be impractical.

The maceration of larvae when ingested by crustacea make specific identification of larvae and estimates of consumption rates difficult. There is some reason for optimism, however, since crustacean predators seem to have low daily consumption rates, and immunological techniques which give only incidence might be useful for assessment of consumption in crustacean predators. These techniques have been used to trace food webs (Boreham and Ohiagu, 1978; Feller, 1982). Laboratory studies are required to check for cross reactions and to determine the duration that larvae can be detected in predator stomachs using immunological techniques.

Accurate estimates of the impact of predators also require that the consumption by predators be measured at the height of the spawning season, and since consumption by predators may increase non-linearly with the abundance of eggs and larvae, measurements of both consumption rates and larval abundance must be done at the same place and time. Eggs and early larvae are sufficiently concentrated at times for predators to feed selectively rather than consuming them incidently with other foods. This seems to be the case for schools of anchovy feeding on their own eggs (Hunter and Kimbrell, 1980a) and may be important for the planktivorous predators of cod as well, but such effects can only be detected by simultaneous plankton and predator catches.

The great variety of potential predators of cod eggs and larvae makes it impractical to study systematically every one. Thus the most reasonable approach is to select several that seem to be the most influential. Such predators must have a high population biomass, a high population consumption rate, and a preference for the size or taxon in question, but still be able to maintain a high abundance on alternative prey and have recruitment that is relatively independent of the prey organism abundance (Rothschild and Rooth, 1982). The planktivorous fishes (herring and sprat) and some of the invertebrates may fit this role for cod eggs and larvae.

The predation problem seems so complex that it may take a long time before mortality rates of cod can be partitioned among the different groups of predators or predator-feeding models tested against accurate field estimates of consumption. Thus, as a first step, it may be preferable to assess the incidence of starvation in the sea, and thereby determine by difference the proportion of total mortality caused by predation. Accurate field work can be done now on starvation using histological critera and growth increments on otoliths, whereas field work on predation has many more uncertainties. In addition, various laboratory studies on predation seem very important to do, including the size-specific avoidance ability of all life stages from egg through metamorphosis using lunging, pursuing, and filter feeding predators; digestion rates of larvae in predator stomachs as a function of larval size; calibration of immunological techiques for detection of predation; and experiments on predation rates in large semi-natural enclosures.

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8441

Synopsis of Culture Methods for Marine Fish Larvae

J. R. Hunter

THE objective of this paper is to provide a synopsis of present technology for small-scale laboratory culture of marine fish larvae. The technology of marine fish culture is relevant to this book because it is one of the best ways to obtain a taxonomic series. "Ahlie" Ahlstrom was a strong proponent of this approach and I lectured on the subject at his request for his courses on larval fish systematics. Marine fish culture has often been reviewed (May, 1970; Houde, 1972a; Houde and Taniguchi, 1979; Shelbourne, 1964; Kinne, 1977) and many additional references may be found in the previous reviews. The key feature of my review is that it is a condensed practical guide and key to the literature for beginners interested in small-scale laboratory culture of marine fish larvae; culture of freshwater fishes is not considered.

EGGS

Sources.—Pelagic fish eggs can be obtained from plankton tows, by catching ripe fish and fertilizing the eggs, and by induction of spawning of laboratory brood stock.

Let eggs taken in plankton tows stand in quart bottles for 0.5 h, then remove plankton from bottom of jar and add fresh sea water (a second decanting may be required). Jars are stored on their sides in an insulated ice box with a refrigerant for 24 h or longer with the temperature kept within spawning range.

Virtually all marine clupeoid fishes (Blaxter and Hunter, 1982) and probably most other pelagic marine fishes spawn at night, hence running ripe fish are more common at night or just before sunset (final egg maturation or hydration occurs just before spawning). After an egg is spawned in sea water its fertility decreases but the maximum time for it to become infertile is highly variable among species, varying from 6 minutes to over 3 hours (Ginzburg, 1972). Sperm in sea water may remain fertile for days (Ginzburg, 1972) although fertility periods as short as 30 seconds have been observed (Haydock, 1971). Owing to the great variation in the time eggs and sperm remain fertile it is preferable that sperm and eggs be mixed immediately after they are obtained.

Storage of gametes may be helpful since mature males and females are not always available simultaneously and crosses between subpopulations may be desired. It is well known that sperm can be stored for extended periods (10 or more hours) if kept cool and maintained in the concentrated form and not activated by sea water (Ginzburg, 1972; Erdahl and Graham, 1980). Fertilization of *Clupea harengus* eggs may be obtained after 6–7 days dry storage at 4° C but a high hatching rate is expected only after periods less than 36 h (Blaxter and Holliday, 1963). It is now possible to extend the life of fish sperm for much longer periods using cryopreservation techniques (−196° C) (Erdahl and Graham, 1980). Various cryoprotective agents have been used to freeze sperm of marine fishes including glycerol (Blaxter and Holliday, 1963), glucose, NaCl, Ringer's solution and fish serum (Hara et al., 1982).

The stress of capture causes female *Katsuwonus pelamis* to ovulate and spawn within 24 h after capture but eggs are often not viable (Kaya et al., 1982). Maturing marine fish in the laboratory and spawning them by hormone injections has become routine in recent years and is preferable to stress techniques. Examples include *Engraulis mordax* (Leong, 1971), *Scomber japonicus* (Leong, 1977), *Chanos chanos* (Liao et al., 1979), *Bairdiella icistia* (Haydock, 1971), *Paralichthys dentatus* and *Pseudopleuronectes americanus* (Smigielski, 1975a, b) and others (see review of Lam, 1982). Induction of spawning in the laboratory may require an open sea water system, large holding tanks (e.g., ~3 m dia. or larger), temperature and light control.

Handling and stocking.—To count eggs without damaging them we recommend a polished wide bore (~3 mm) pipette; count 30–50 late stage eggs at a time in a depression slide under a dissection microscope, and wash eggs off the slide by immersion of the entire slide in sea water. Counting eggs is critical because higher mortalities and slower growth result from excess stocking densities (Houde, 1975 and 1977). As a rule stocking densities in rearing tanks of 8 eggs/l or less seems preferable and most rearing successes have occurred when stocking did not exceed 20 eggs/l (Houde, 1975). Similarly, the mortality of *Mugil cephalus* larvae seems to remain constant (2–3% loss/day) at stocking densities of 1–30 larvae/l (Kraul, 1983).

APPARATUS

Containers and lighting.—Larvae appear to grow faster and show fewer signs of starvation when reared in large containers (100 l) rather than in smaller ones (10 l) (Theilacker, 1980b). Optimum container size doubtless varies with species but 40 l containers are probably the minimum size that should be used and I prefer 100–400 l containers. We use cylindrical black fiberglass containers although excellent results are obtained using ordinary rectangular glass aquaria (Houde, 1975).

It is traditional to provide a daily cycle of illumination to larvae in rearing containers although constant illumination is occasionally used. Typically fluorescent lamps are used which provide 2,000–3,000 lux at the water surface (Houde, 1978; Hunter, 1976). Night light levels vary; we provide no light at night whereas Houde (1978) provides a dim light of 40–90 lux at night, which is substantially above the visual threshold for feeding for larval *E. mordax* (6 mm larvae 50% feeding threshold = 6 lux, and 10–15 mm larvae 50% threshold = 0.6 lux, Bagarinao and Hunter, 1983). Clearly, longer periods for visual feeding will probably enhance growth if food is limited. Rearing at high light intensities such as natural sunlight may greatly increase production of algae and zooplankton in the culture tank and thereby increase larval survival (Kraul, 1983). On the other hand, solar UV radiation is clearly lethal to younger larvae (Hunter et al., 1982) and use of deep tanks, or shaded or covered tanks (screen cloth, acrylic plastic, glass or mylar film) is recommended for the first 1–2 weeks of larval life if tanks are to be exposed to solar radiation.

Water quality.—Closed, non-circulating systems are typically used to rear marine fish larvae at least during the younger stages, because in an open system planktonic larvae and their foods are easily lost. Older (nektonic) larvae are able to resist the current and to consume a daily ration in a short period so a partially open system can be used. We fill our rearing containers with UV treated sea water that is passed through three, in line, cartridge filters (5, 3 and 1 μm pore).[1] Although not a common practice in small scale rearing work, the addition to rearing tanks of antibiotics (sodium penicillin G at 50 i.u./ml plus streptomycin sulphate at 0.05 g/ml) slightly improved survival of *Pleuronectes platessa* eggs through hatching, but surprisingly this single treatment greatly improved survival of larvae through metamorphosis (Shelbourne, 1975).

Use of a closed system requires attention to water quality, a problem which may be intensified at higher rearing temperatures. In the most complete study of water quality in rearing tanks for marine fish larvae, Brownell (1980a, b) considered seven variables (pH, dissolved oxygen, carbon dioxide, ammonia, nitrite and nitrate), but only high pH, low dissolved oxygen and un-ionized ammonia had effects at levels likely to be encountered in rearing tanks. First feeding incidence declined by 50% in all species he studied when dissolved oxygen concentrations were between 4 and 4.75 mg/l (49–58% saturation). Dissolved oxygen in our rearing containers usually is not saturated after planktonic foods are added, and typically it is about 80% saturation even with aeration. Clearly water quality is improved by aeration and frequent water changes and tank cleaning. Werner and Blaxter (1980) exchanged 20% of the water in *Clupea harengus* cultures (9° C) 3 times per week but at high temperatures greater replacement rates are required. For example Houde (1977) replaced 20% of the tank sea water on alternate days while culturing *Anchoa mitchilli* and *Achirus lineatus* at 26–28° C. Frequent tank cleaning is important as heavy mortalities may result from toxins produced by debris on the container bottom (Kraul, 1983). Aeration, unless very gentle, can cause heavy mortalities among delicate eggs and newly hatched larvae. In fact, Shelbourne (1964) recommends no aeration for *Pleuronectes platessa* larvae. I recommend very gentle aeration but not until a week or so beyond the first feeding stage.

The mortality of cultured fish larvae often increases during the period of initial swim bladder inflation in physoclistous fishes (Doroshev et al., 1981; Kuhlmann et al., 1981) and this could be related to water quality. Symptoms include delay or complete failure of inflation or excessive inflation; in either case normal swimming patterns are disrupted and death frequently results. The causes of abnormal inflation are not clear; prevention of larvae from reaching the water surface prevented excess inflation in *M. cephalus* larvae (Nash et al., 1977), whereas the same treatment in *Atractoscion nobilis* larvae had no effect. In *A. nobilis* excess inflation was associated with abnormal development of gas secretory tissue suggesting a more complex etiology (SWFC, unpubl. data). Failure to inflate the swim bladder is a common problem in *Morone saxatilus* culture and turbulent aeration may reduce the incidence of this disease (Doroshev and Cornacchia, 1979) but it now appears that reduction in salinity from 17 ppt to 4 ppt has a much greater effect in reducing the incidence of swim bladder malfunction (S. Doroshev and J. Merritt, U. Cal. Davis, pers. comm.).

FOOD

The most critical aspect of rearing marine larvae is management of their food. Food must be the correct density, size, nutritionally adequate and must remain suspended in the water column which usually requires the use of living pelagic organisms.

Food size.—Typical pelagic fish larvae are 2.5–4.0 mm when they begin feeding and acceptable prey are 20–150 μm in breadth (Houde and Taniguchi, 1979). Some large larvae, e.g., larval *C. harengus* (Blaxter, 1965), *Pleuronectes platessa* (Riley, 1966) or small larvae with large mouths, e.g., *Merluccius productus* (Sumida and Moser, 1980), can begin feeding on prey 300 μm or larger in breadth. The optimal food size increases as larvae grow (Hunter, 1981), so any culture technique should provide a steadily increasing range of food sizes, because if the food is too small growth slows and mortality occurs (Hunter, 1981). Food size requirements can be expressed in terms of the ratio of prey width to mouth width. The 50% threshold for feeding on a prey of a particular width occurs when this ratio is about 0.75, although occasionally larvae consume prey as wide as the width of their mouth (ratio = 1) (Hunter, 1981). At the onset of first feeding a small prey of about ¼ the mouth width seems to be preferable as capture success is low at this time but within a few days larvae are able to consume food of about ½ the mouth width.

Wild zooplankton.—Wild zooplankton, primarily the naupliar and copepodite stages of marine copepods but also mollusc veligers, tintinnids, cladocera, and appendicularia larvae, are the natural foods of most marine fish larvae and probably also the best source of food for rearing a larval taxonomic series. Wild zooplankton provide a wide range of sizes and types and are probably nutritionally superior to cultured rotifers and *Artemia* nauplii (Kuhlmann et al., 1981). Collection of wild zooplankton may require less effort than production of cultured food except for brine shrimp nauplii (see below). Zooplankton is collected in nets of about 50 μm, and is graded by size in the laboratory using various nylon nets (Houde, 1977, 1978). This eliminates the larger zooplankton which larvae would be unable to consume and which may be larval predators. Fish larvae, particularly yolk-sac stages, are vulnerable to various carnivorous copepods, amphipods, euphausiids and chaetognaths (Hunter, 1981).

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[1] Aqua-Pure model AP10, AMF Cuno Division, Inc., Meriden, Connecticut USA.

Cultured foods.—Two cultured foods, the rotifer *Brachionus plicatilis,* and nauplii of the brine shrimp, *Artemia,* should be considered as potential foods for rearing marine fish larvae as many fish larvae can be reared on a combination of these two foods. These two foods may also be used as a supplement to diets of wild plankton. Groups of fishes that have been reared to metamorphosis on a combination of *Brachionus* and *Artemia* or on *Artemia* alone include *C. harengus,* species of serranids, scombrids, atherinids, various flatfishes, sciaenids, and saganids (May, 1970; May et al., 1974; and unpubl. SWFC data). *Artemia* nauplii are recommended only for larvae with differentiated guts as they are quite resistant to digestion whereas copepods are not (Rosenthal, 1969).

Methods for culturing rotifers using algae are given by Theilacker and McMaster (1971); culture methods employing formulated artificial diets or freeze dried algae (Gatesoupe and Robin, 1981; Gatesoupe and Luquet, 1981) and ones using brewers yeast also exist. Many of the essential facts given in these original papers will not be repeated here but I will point out a few practical points regarding rotifer culture using algae. Suitable algae species for rotifer culture include *Dunaliella, Nannochloris, Tetraselmis,* and *Chlorella* which may be grown using standard culture media (Guillard, 1975) or using liquid commercial plant fertilizers (dosage for fertilizer containing 8% total nitrogen = 0.1 ml of fertilizer/l; dosage among brands is adjusted depending on total N content). We prefer commercial plant fertilizers that have an organic base such as liquid fish fertilizers and avoid those that have soil penetrants. A daily doubling rate can be expected in healthy rotifer cultures, and cultures can be maintained for weeks or even months by adding fresh algae or nutrients and sea water, although single batch harvesting after about 2 weeks gives more dependable results. Rotifers are harvested using gravity flow through a nylon filter (20–40 μm mesh) as pumps may kill rotifers.

Production of *Artemia* nauplii is simple since all that is needed is to hatch the cysts ("*Artemia* eggs"). Cysts from a variety of strains of *Artemia* are commercially available. The strains differ considerably in average naupliar size (423–775 μm length), in pesticide content (DDT, PCB, and chlordane) and in certain fatty acids (Klein-MacPhee et al., 1982). These authors show that very low survival (15%) of *P. americanus* larvae occurred when they were fed San Pablo Bay (San Francisco) nauplii whereas survival of larvae fed other strains varied from 60–80%. Beck et al. (1980) gave similar results for *Menidia menidia* larvae. Of all the strains tested in these papers the Australian and Brazilian strains seem the most suitable for rearing larvae and the San Pablo Bay (USA) the least.[2]

Artemia hatcheries vary from a jar to complex automated systems. The J. D. Riley *Artemia* hatching box has been used with slight modification in many laboratories for over 20 years. It is a sea water filled box separated in half by a sliding partition; *Artemia* cysts are added to one side (1 g/l) and they hatch 1–2 days later depending on the temperature selected (23–30° C). The tank is then illuminated, the partition raised slightly off the bottom, and the nauplii, attracted by the light, swim beneath the partition leaving behind the hatching debris and unhatched cysts (Shelbourne, 1964). A semiautomatic version of this system is described by Nash (1973), and various other improvements in aeration, illumination, temperature, and other factors have increased yields to 10^6 nauplii per 4.8 g of cysts (San Francisco Bay Brand) (Dye, 1980). In recent years decapsulation of *Artemia* cysts using hypochlorite bleach has become popular because it increases yields, increases the dry weight of the nauplius (Bruggeman et al., 1980) and eliminates contamination of larval fish rearing tanks with unhatched cysts.

It should also be noted that freshly hatched *Artemia* nauplii are clearly more nutritious than older starving individuals and consequently new batches should be frequently produced. In general, prey with full stomachs are probably nutritionally preferable to ones with empty stomachs. Similarly, more *Dicentrarchus labrax* larvae seem to survive when rotifers are nutritionally enhanced by 30 min immersion in a solution containing vitamins and soluble proteins (Gatesoupe and Luquet, 1981).

Mass culture of marine copepods is difficult and laborious and therefore not recommended when a taxonomic series is the sole objective. Nevertheless, culture of marine copepods may be the only way some fish larvae can be reared if wild zooplankton is not readily available and larvae die when fed *Artemia* nauplii (rarely are more than a single strain of *Artemia* tested, however). Harpacticoid copepods (*Tigriopus* sp., *Tisbe* sp., and *Euterpina* sp.) are the most frequently used copepods because of ease of culture; for culture techniques see Kahan et al. (1982) and Hunter (1976). *Euterpina* may be preferable to *Tigriopus* or *Tisbe* because the nauplii and copepodites of *Euterpina* are pelagic and therefore available to the larvae whereas nauplii and copepodites of *Tigriopus* and *Tisbe* tend to remain on surfaces and are therefore less available (Kraul, 1983). See Nassogne (1970) and Zurlini et al. (1978) for laboratory culture of *Euterpina.*

Food density.—The optimal food density for fish larvae depends upon the size of the food organism and size or age of the larvae. Densities of 1–3 organisms/ml have been routinely used for larvae fed wild zooplankton (largely copepod nauplii) during the first 1–2 weeks of feeding (Houde and Taniguchi, 1979). The same density range is used when cultured *Artemia* nauplii are the food. A higher density range (10–20/ml) is used for cultured *B. plicatilis* which are about 1/10 of the weight of an *Artemia* nauplius (Theilacker and McMaster, 1971). A very small food particle, the dinoflagellate *Gymnodinium splendens* (40 μm dia), is used for the first 2 days of feeding in northern anchovy larvae (Lasker et al., 1970; Hunter, 1976) at a high density of about 100/ml. In very active species such as *S. japonicus* or the siganid *Siganus canaliculatus* high food densities can cause heavy mortality because of overfeeding since most larval fishes seem to lack a satiation mechanism (May et al., 1974; Hunter, 1981). Overfeeding seems to occur only when such easily captured prey as *Artemia* nauplii are used as food.

Piscivorous fish larvae.—Piscivorous fish larvae such as the scombroids, *Sphyraena* and others pose special problems in culture. Fish larvae are an ideal food for such larvae; in fact, our only success in rearing *Katsuwonus pelamis* larvae to metamorphosis was probably related to an abundant supply of yolk-sac fish larvae as food. Zooplankton is the initial food until piscivorous feeding habits develop (Houde, 1972b; Mayo, 1973; Hunter and Kimbrell, 1980). Piscivorous larvae manipulate their larval prey and consequently are less dependent on mouth size when consuming larval fish. Sibling cannibalism is common under rearing conditions in such fishes. Increasing the food density may increase survival as may elevating the temperature, thereby accelerating growth through the most cannibalistic sizes; at least in scombroids sibling cannibalism declines at metamorphosis (Mayo, 1973; Hunter and Kimbrell, 1980). Sorting by size and isolating the larger larvae is probably the only certain method for controlling losses due to cannibalism, however.

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[2] Exotic *Artemia* cysts are available from: Artemia Inc., P.O. Box 2891, Castro Valley, California 94546 USA and Biomarine Research, 4643 W. Rosecrans, Hawthorne, California 90250 USA.

PHYTOPLANKTON

Phytoplankton blooms are often maintained in larval culture tanks to reduce the detrimental effects of metabolic by-products which accumulate in static rearing tanks (Houde, 1974) and to provide food for larval food organisms. In many cases dense blooms of phytoplankton enhance larval growth and survival and I recommend the practice but the mechanism is obscure. The phytoplankters used are various, easily grown, small species such as *Chlorella, Anacystis, Nannochloris, Tetraselmis, Dunaliella, Isochrysis, Phaeodactylum* and others.[3] They are maintained at high densities (10,000 or more cells/ml) in the rearing tanks. At high cell densities larvae ingest these small phytoplankters, perhaps inadvertently (Moffatt, 1981) but they appear not to be able to exist on them as a sole food source (Houde, 1974; Scura and Jerde, 1977). They may supplement the food ration either directly or indirectly through the ingestion of prey having guts full of algal cells (Moffatt, 1981). Evidence now exists that enhancement of growth and survival of larval *Scophthalmus maximus* by blooms of *Isochrysis* and *Phaeodactylum* is due to the inclusion in the diet of certain polyunsaturated fatty acids not occurring in the normal laboratory rotifer diet (Scott and Middleton, 1979). It is interesting in this regard that *Dunaliella* which lacks the fatty acids did not enhance *S. maximus* larval growth or survival.

EFFECTS OF CULTURE

Extrapolation from cultured larvae to natural populations must be done with caution because culture may affect the morphology, behavior and biochemistry of larvae (Blaxter, 1976). The morphological characteristics most susceptible to modification in tanks are those partially controlled by environmental conditions such as vertebrae and fin ray counts. Reared larvae also may be more heavily pigmented than sea caught specimens (Watson, 1982). This appears to be related to the expanded nature of the melanophores, not to added numbers of pigment cells. In addition, pigmentation events may occur at smaller sizes in reared material (S. Richardson, Gulf Coast Research Laboratory, Ocean Springs, Mississippi, pers. comm.). Laboratory reared larvae are often heavier and have deeper bodies than their wild counterparts, making some morphometric measurements on laboratory specimens useless (Blaxter, 1975). The differences in preservation and handling between laboratory and sea-caught larvae also make direct size-specific comparisons difficult. Shrinkage in length may vary greatly depending on the duration larvae remain in plankton nets and shrinkage differences between reared and wild specimens can be misinterpreted as morphological differences (Theilacker, 1980a).

NATIONAL MARINE FISHERIES SERVICE, SOUTHWEST FISHERIES CENTER, P.O. BOX 271, LA JOLLA, CALIFORNIA 92038.

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[3] For a nominal fee starter cultures of marine phytoplankton can be obtained from R. R. L. Guillard, Bigelow Laboratory for Ocean Sciences, McKown Point, West Boothbay Harbor, Maine 04575 USA; culture methods are discussed by Guillard (1975).

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RATES OF ATRESIA IN THE OVARY OF CAPTIVE AND WILD NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

J. ROE HUNTER AND BEVERLY J. MACEWICZ[1]

ABSTRACT

The process of ovarian atresia was described for northern anchovy using a laboratory group in which atresia was induced by starvation. Atretic characteristics of the ovary were described and illustrated, atretic ovarian states defined, and the rate that the ovary passed from one atretic stage to another was measured. The ovaries of starved females regressed rapidly; 3 days after the onset of starvation the ovaries of about half of the females contained yolked oocytes undergoing resorption of yolk (alpha stage of oocyte atresia) and by 23 days after the onset of starvation no yolk remained in the ovaries of any of the females. Gamma + delta stages of atretic follicles persisted in the ovary for over a month, but their decline in abundance indicated that eventually all signs of past reproductive activity would be lost in regressed ovaries.

In the natural population, rates of ovarian atresia increased seasonally from only a few percent of the females showing some atresia in peak spawning months to over 50% near the end of the season. Females with low levels of alpha stage atresia (< 50% yolked oocytes affected) spawned about half as frequently as did those with no alpha stage atresia. Spawning was rare (1% of the females) or absent in females with high levels of alpha stage atresia (> 50% yolked oocytes affected). Late in the spawning season, it may be possible to forecast the end of spawning in the populations using the frequency of females in the populations with high levels of alpha stage oocyte atresia. Throughout the spawning season atretic rates were higher in small females (standard length < 10 cm) than in larger ones indicating that 1-year-old females spawning for the first time have a much shorter spawning season than do older females.

Four approaches commonly used to determine the reproductive state of female fishes are 1) staging of ovaries using gross anatomical criteria such as the international Hjort scale (Bowers and Holliday 1961); 2) calculation of the gonosomatic index (GSI), i.e., gonad weight divided by female weight or the equivalent (de Vlaming et al. 1982); 3) estimating the mean diameter of the oocytes in the most advanced mode of oocytes (Hunter and Goldberg 1980; Hunter and Leong 1981); and 4) classifying ovaries histologically. Histological classification is superior to all other methods. Two of its great strengths are that the frequency of spawning of multiple spawning fish populations can be accurately estimated using the presence of postovulatory follicles (Hunter and Goldberg 1980) and that regressing ovaries can be distinguished from immature and from postovulatory ovaries. The histological criteria used to identify regressing ovaries is the presence of many oocytes and follicles undergoing resorption, a process known as atresia.

The interpretive power of histological analysis could be enhanced if the process of ovarian atresia were better documented. Specifically, ovarian atretic stages need to be defined, rates of atresia and duration of stages estimated, and the relation between ovarian atretic state and the probability of spawning determined. Such information would facilitate process oriented field studies on reproductive biology, and increase the accuracy of estimates of size at first maturity and size- or age-specific duration of the annual spawning season.

This study provides the laboratory and field calibration necessary for the assessment of the reproductive state of northern anchovy, *Engraulis mordax*, using the atretic condition of the ovary. We identify a range of ovarian atretic characteristics that define the atretic condition of the ovary, estimate rates of atresia, and estimate the duration that atretic characters persist in the ovaries of starving females in the laboratory. We use this information to classify ovaries of sea-caught females and estimate the probability of spawning for females with various levels of ovarian atresia.

We know of no similar work. A large descriptive

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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literature exists on follicular atresia in fishes (reviewed by Saidapur 1978) and stages of atretic oocytes and follicles have been defined (Bretschneider and Duyvene de Wit 1947; Lambert 1970a), but only the atretic rates in the guppy have been measured (Lambert 1970a). Considerable attention has been devoted to stages of atretic follicles (corpora atretica or "preovulatory corpora lutea") because of a presumed endocrine function (see reviews by Hoar 1965; Byskov 1978). The seasonal occurrence of atretic oocytes and follicles is often discussed as part of a general description of seasonal changes in the ovary of marine fish; see, for example, cycles described for the gobiid, *Gillichthys mirabilis* (de Vlaming 1972); plaice, *Pleuronectes platessa* (Barr 1963); *Paracentropristis cabrilla* (Zanuy 1977); and three species of *Epinephelus* (Bouain and Siau 1983). The proportion of females with atretic ovaries or the numbers of atretic oocytes within the ovary is given less often, but a few reports exist. For example, atresia ranged from 0 to 6% of the oocytes in female haddock, *Melanogrammus aeglefinus* (L.) (Robb 1982); corpora atretica increased to about 3% of the oocytes during the postspawning period of the dab, *Limanda limanda* (L.) (Htun-Han 1978); and atretic oocytes varied from 13% of yolked oocytes during the prespawning period to 100% during the postspawning period of the snapper, *Chrysophrys auratus* (F.) (Crossland 1977). Some attention has been given to the issue of whether or not atretic rates can account for differences in fecundity among females fed high and low rations. It appears that ration-related differences in fecundity are more closely tied to production rates of oocytes rather than atretic rates (Tyler and Dunn 1976; Wootton 1979). In summary, our literature review indicates that ovarian atresia has yet to be used for quantitative estimation of any reproductive processes in marine fish populations, although it has been used in general descriptions of the seasonality of reproduction for many years.

METHODS

Laboratory Experiment

Adult northern anchovy captured by commercial bait fishermen on 23 February 1982 were kept in a live car in San Diego Bay. Three days later about 1,000 fish averaging 104 mm SL (9.50 g) were taken to the laboratory and held in a 4.6 m diameter pool (1 m deep) at which time the first fish sample was taken. Over the first 34 d in captivity, samples of 18-24 females were taken at 3-4 d intervals with the final sample taken after 62 d in captivity. The temperature of the seawater ranged from 15.5° to 16.5°C.

The fish were not fed during the first 27 d in captivity because starvation was used to trigger the resorption of the ovary; thereafter they were fed daily. On the 27th day of starvation the ovaries had regressed from 4% of female body weight to 0.8% and feeding was resumed because we wished to learn how long the atretic characters would last once the fish began to feed.

In our calculations of atretic rates of laboratory females, we assumed that all the females at the time of capture had active ovaries without atresia, although no samples were taken until 3 d after the fish were captured. Only 3% of the 1,680 females taken in a survey conducted at the same time (28 January-8 March 1982) had atretic ovaries, and it was prominent in only 0.1% of the females (50% or more of yolked oocytes were affected). Ninety-six percent of the females in our first sample (taken 3 d after capture) had yolked eggs, and half of them had no atresia.

All females sampled during the course of the laboratory experiment were weighed and measured, and the ovary removed, weighed, and a section removed for histological analysis. Ovaries were fixed in 10% neutral buffered Formalin[2] and embedded in Paraplast. Histological sections were cut at 6 μm and stained with Harris hematoxylin followed by eosin counterstain.

Sea Data

The ovaries of northern anchovy taken in trawl surveys used for biomass estimation (Stauffer and Picquelle[3]) and various other collections from commercial seiners and midwater trawls were histologically examined. The number of females examined per catch (trawl, purse seine, or lampara net) has varied from 10 to 20. Some collections were quite small, especially those taken outside the main spawning season in the Southern California Bight; these small collections may consist of only two catches, whereas those taken during the main spawning months (February-March) were large, often consisting of 100 or more catches of 10-20 females each. In all collections ovaries were classed according to atretic characteristics as well as on the basis of the presence of postovulatory follicles (age 0 and age 1 d) and hydrated eggs according to the method described by Hunter and Goldberg (1980). All but two of the collections were from the Southern California Bight or northern Baja California, the region where the Central subpopulation of the northern anchovy is concentrated (Vrooman et al. 1981). Two collections were from the vicinity of Monterey and San Francisco Bays. Fish from these areas appear to have a different spawning season from those of fish to the south so they are listed separately in our seasonal tabulations. All collections were classified using histological criteria to determine the incidence of ovarian atretic states as a function of female size, season, and reproductive state.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3] Stauffer, G., and S. Picquelle. The 1980 and 1981 egg production estimates of anchovy spawning biomass. Unpubl. manuscr. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Histological Characteristics

We describe below the histological characteristics of four oocyte classes and four stages of atresia in the northern anchovy. These stages and classes are subsequently used to define various ovarian atretic states in laboratory and sea-caught female anchovy.

Oocyte Classes

The northern anchovy is a multiple spawning fish (Hunter and Goldberg 1980) with asynchronous oocyte development (oocytes in many stages of development occurring simultaneously in reproductively active ovaries; Wallace and Selman 1981). During the spawning season oocyte development is a continuous process involving all stages with a new spawning batch maturing every week to 10 d (Hunter and Leong 1981). Oocyte development and maturation in teleosts, reviewed recently by Wallace and Selman (1981), has frequently been subdivided into many stages (Andrews 1931[4]; Yamamoto 1956; Lambert 1970b), but our work required a simpler histological classification system. We have combined the stages of past authors into four oocyte classes (unyolked oocytes, partially yolked oocytes, yolked oocytes, and hydrated oocytes), and we describe the histological characteristics of each class below.

1) Unyolked Oocytes—This class includes all oocytes without yolk that are about 0.04 mm or larger and range upward in size to about 0.35 mm (U, Fig. 1a, b). Oocytes <0.04 mm are excluded because they consist mostly of "oogonium nests", do not have a true follicle layer, and do not seem to undergo degeneration (o, Fig. 1b). The smaller oocytes within this class (0.04-0.15 mm) are spherical, have a large nucleus with a narrow homogenous very densely staining cytoplasm (Fig. 1b). A very thin single layer of elongated, spindlelike cells (the beginning of the granulosa layer) surrounds these small oocytes. The large oocytes in this class are oval, the cytoplasm stains faintly with hematoxylin and has a cloudy, mottled appearance (Fig. 1d). The oval nucleus of these oocytes contains several nucleoli and is surrounded by a granular perinuclear zone. In these larger oocytes a thin, definite, faintly eosinophilic staining, hyaline membrane (precursor of the zona radiata) appears between the oocyte and the growing follicle. The follicle consists of a narrow single inner layer of cuboidal granulosa cells and a single outer layer of flat elongated thecal cells with some blood capillaries. The larger oocytes also may have some small vesicles in the periphery of the cytoplasm. These vesicles are at times difficult to distinguish and they seem to disappear in yolked oocytes. No oil vacuoles exist as northern anchovy eggs do not contain oil droplets.

2) Partially Yolked Oocytes—Oocytes in this class are in the early stages of yolk deposition (vitellogenesis) and range in size from 0.3 to 0.5 mm (major axis) (P, Fig. 1d, g). The class includes oocytes in the initial stage of yolk deposition up to and including those in which yolk granules or spherules extend three-fourths of the distance from the periphery to the perinuclear zone. Yolk deposition starts at the periphery of the oocyte cytoplasm as small eosinophilic staining granules and then subsequently spreads internally until they nearly reach the finely granular perinuclear zone. Usually by this time the granules have become small spherules. The oval-shaped nucleus of oocytes in this class contains several nucleoli. Delicate striations appear on the hyaline membrane between the oocyte and follicle layer at the time yolk appears in the oocyte. As maturation proceeds, the follicle layer becomes wider due to an increase in the width and proliferation of granulosa cells. The thecal cells do not increase in size but remain elongated, flat cells with occasional blood capillaries and form a thin outer cov-

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[4] Andrews, C. B. 1931. The development of the ova of the California sardine (*Sardina caerulea*). Unpubl. manuscr., 88 p. Stanford Univ., Stanford, CA 94305.

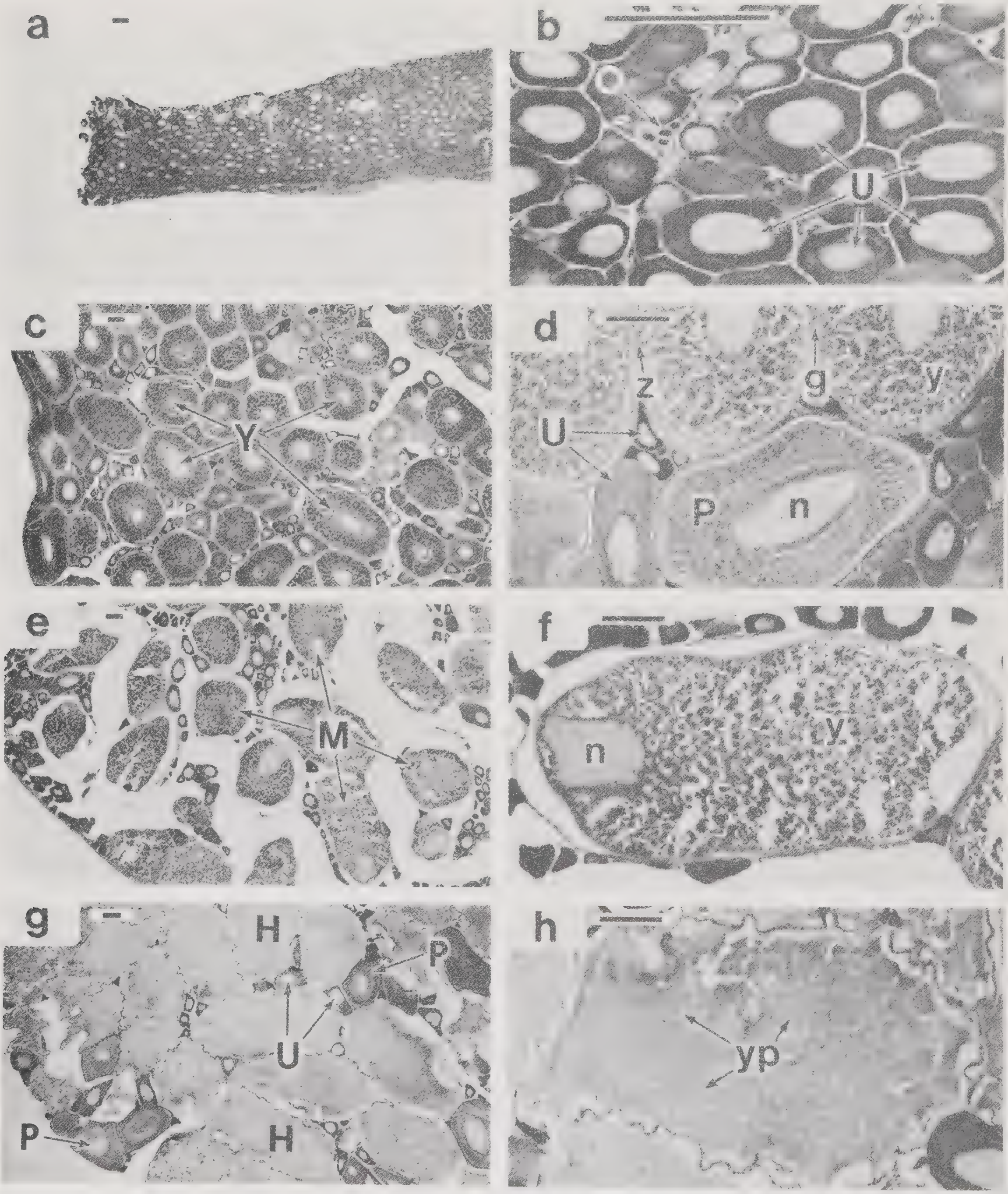

FIGURE 1.—Development of northern anchovy ovary at various magnifications (stain = H & E, bar = 0.1 mm). a) Immature ovary consisting of unyolked oocytes and no atresia. b) Enlargement of (a) showing small spherical unyolked oocytes (U) with a large central nucleus and "oogonium nests" (o). c) Normal mature ovary with many fully yolked oocytes (Y). d) All stages of oocytes: unyolked (U), partial yolked (P), and yolked (Y), are present in normal mature ovaries. (g = granulosa cell layer, z = zona radiata, n = nucleus, y = yolked globules.) e) Prespawning ovary showing migration of nucleus to the animal pole. f) Enlargement of a migratory nucleus oocyte (M). (n = nucleus, y = yolk globules.) g) Imminent (<12 h) spawning ovary with hydrated oocytes (H) still within the follicle layer. (U = unyolked, P = partial yolked.) h) Enlargement of a hydrated oocyte. Note that the yolk globules have fused into yolk plates (yp) and there is no prominent nucleus due to disintegration of the nuclear membrane.

ering to the follicle. The thecal cells do not change until hydration when they become even flatter and have a stringy appearance.

3) Yolked Oocytes—Oocytes in this class range from 0.45 to 0.80 mm (major axis), and all contain yolk spherules or globules throughout the region between the periphery of the oocyte and the perinuclear zone (Y, Fig. 1c, d). As vitellogenesis continues, the yolk varies from spherules in the smaller oocytes to large globules in the larger ones. Just prior to spawning (<24 h) the globules fuse to form yolk plates (Fig. 1h). Such oocytes are excluded from this oocyte class, this characteristic being diagnostic of the last class (hydrated oocytes). The nucleus of oocytes in the yolked oocyte class is oval with numerous nucleoli. The granulosa cells have a wide rectangular shape in cross section and a large oval nucleus; their walls are clearly evident in sagittal section where they form polyhedrons. The zona radiata is a wide, striated, eosinophilic band until hydration when it stretches thin and the striations disappear.

4) Hydrated Oocytes—These oocytes range in size from 0.75 to 1.2 mm (major axis) (H, Fig. 1g, h). Hydration (rapid uptake of fluid by the follicle, Fulton 1898) begins when the nucleus has migrated to the animal pole (M, Fig. 1e, f) and yolk globules first fuse to form yolk plates, and it ends when the hydrated oocyte is ovulated. The nucleus of hydrated oocytes is not visible except in the earliest phase because after the nucleus migrates, the nuclear membrane disintegrates dispersing its contents into the cytoplasm. During hydration all yolk globules fuse into plates and the oocyte expands greatly, stretching the granulosa and thecal cell layers. At this time, the granulosa cells in cross section appear as long, thin rectangles, the thecal cells are extremely flat and have a stringlike appearance, and the zona radiata is very thin and lacks striations. Hydrated oocytes are the most ephemeral of all oocyte classes since this stage lasts for less than a day, whereas the other stages are always present in reproductively active anchovy ovaries. Migratory nuclei may be seen as early as 24 h before ovulation, but hydrated oocytes in which all globulues are fused to form yolk plates do not occur earlier than 12 h before spawning. We have never observed atresia in hydrated oocytes; apparently, in northern anchovy, nearly all hydrated oocytes are ovulated.

Atretic Stages

The nomenclature and general characteristics used for the four atretic stages given below follow those of Bretschneider and Duyvene de Wit (1947) and Lambert (1970a). In the initial stage of the atretic process (alpha (α)), the entire oocyte is resorbed including the yolk, if present, by the hypertrophying granulosa cells of the follicle. In the next stage (beta (β)), the major degeneration and resorption of the follicle (granulosa and thecal cells) occurs. In the third (gamma (γ)) and fourth (delta (δ)) atretic stages, regression of the theca and granulosa cells continues, greatly reducing the size of the follicle, and a yellow-brown pigment appears. The histological characteristics used to identify these stages are outlined below.

1) Alpha (α) Stage Atresia—In the alpha stage of atresia the oocyte is resorbing leaving only the follicular layers. The early phase of alpha stage atresia is characterized by the disintegration of the nucleus, evident by an irregular shape, and a granular, dark basophilic staining, and the disintegration of some of the yolk globules, indicated by less refractive globules, fused globules, or globules expanded and of less regular shape (Fig. 2a, b, c). The zona radiata slowly dissolves as indicated by the loss of striations and uneven diameter (Fig. 2b). In subsequent phases of alpha atresia, granulosa cells enlarge and, upon rupture of the zona radiata, invade the degenerating oocyte (Fig. 2d). Yolk adjacent to the invading granulosa cells liquifies (loses all structural integrity and appears as a homogeneous eosinophilic area) and becomes phagocytized by the granulosa cells as indicated by the presence of yolk in the vacuoles of these cells. The basophilic staining cytoplasm is also resorbed by the granulosa cells. In the alpha stage of atresia, blood capillaries and vessels are numerous in the thecal connective layer which does not proliferate or invade the oocyte but remains as a thin layer covering the granulosa cells. The alpha stage ends when resorption of the oocyte is complete (all cytoplasm and yolk are gone). The resulting structure (beta stage) is usually much smaller than the original oocyte. The subsequent atretic stages (beta-delta) are steps in the resorption of the remaining follicle and the structure at this point is called an atretic follicle, the term atretic oocyte being reserved for only the alpha stage of atresia.

In unyolked oocytes the alpha stage process is similar but without yolk (Fig. 2e, f). The nucleus

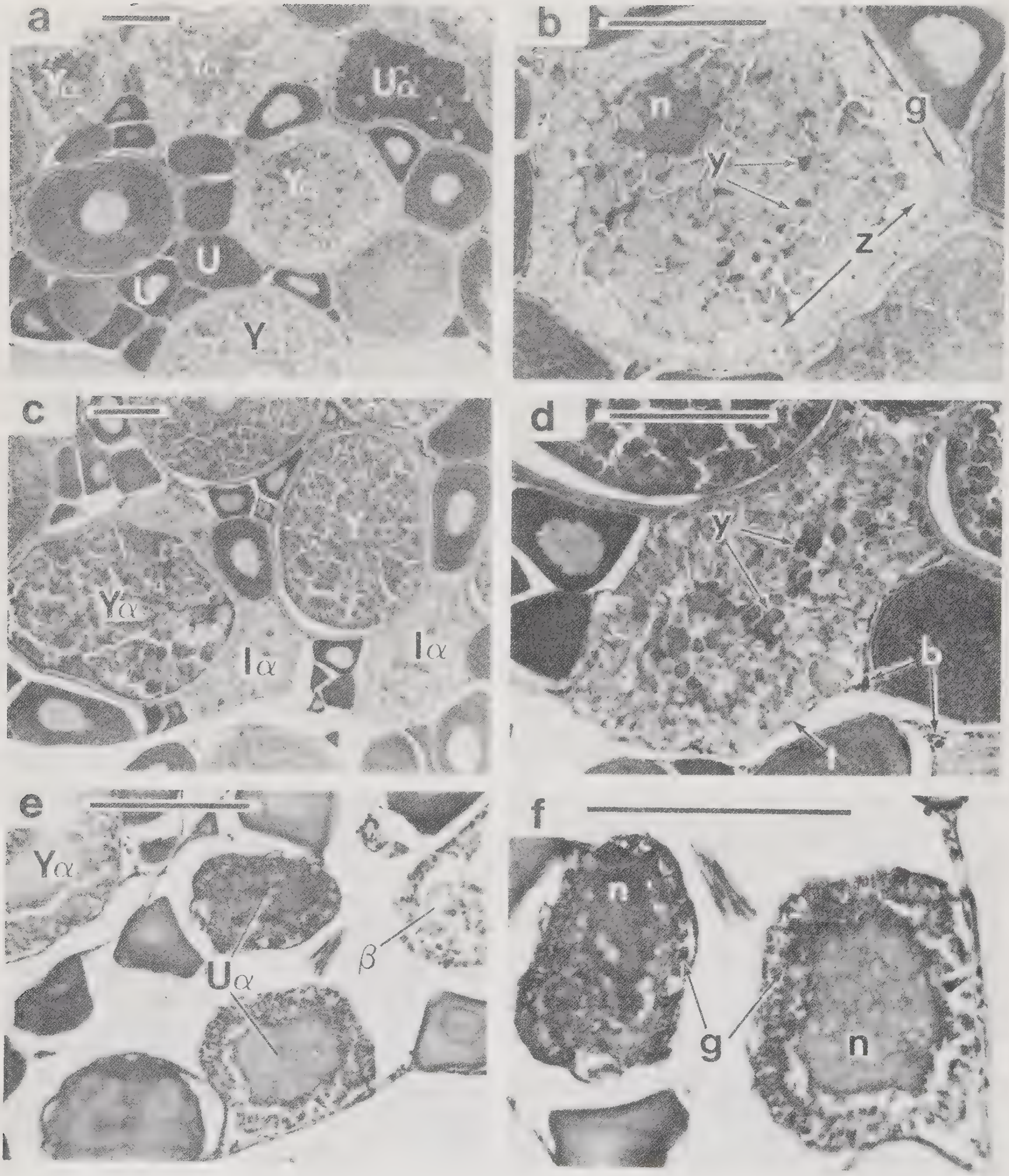

FIGURE 2.—Alpha (α) stage atresia in yolked (Y) and unyolked (U) oocytes (bar = 0.1 mm). a) and b) Yolked oocyte undergoing alpha atresia (Yα). Notice dark irregular nucleus (n), uneven dissolving zona radiata (z), and hypertrophic granulosa cells (g); (Uα = alpha atresia of a large unyolked oocyte). c) and d) Only remnants of yolk (y) remain among the invasive phagocytizing granulosa cells in this late phase of alpha atresia (lα). Note also the thecal layer (t) and the closely associated red blood cells (b). e) and f) Unyolked oocytes in the alpha stage of atresia (Uα), note enlargement of granulosa (g) and disintegration of nucleus (n). (Yα = alpha yolked atretic oocyte, β = beta atresia.)

disintegrates, the thin prezona radiata (if present) dissolves and the granulosa cells enlarge, and, with only a slight proliferation, phagocytize the unyolked oocyte. When resorption is complete, all that remains is the follicle.

2) Beta (β) Stage Atresia—Initially the beta stage atretic follicle is a compact structure composed of numerous disorganized granulosa cells surrounded by a thin thecal and blood vessel layer. The nucleus of some of the granulosa cells is pycnotic and many of the cells contain a large intracellular vacuole that may be empty or contain amorphous particles. Occasionally one or more large intercellular cavities may exist among the granulosa cells (Fig. 3b, d). Preovulatory beta stage atretic follicles containing such cavities may easily be confused with postovulatory follicles (older than 48 h) and, as a consequence, we do not age postovulatory follicles older than 48 h (Hunter and Goldberg 1980). In addition, small (older) beta stage atretic follicles from yolked oocytes (Fig. 3c, d) are indistinguishable from beta stage atretic follicles from unyolked oocytes. Thus, we do not identify the original oocyte type undergoing atresia in beta or subsequent atretic stages; such distinctions are made only for alpha stage atretic oocytes.

Three different patterns of atresia may occur at the conclusion of the beta stage: 1) The follicle may follow the classic pattern outlined by Bretschneider and Duyvene de Wit (1947) and pass through subsequent gamma and delta stages (both characterized by increased pigmentation, see below); 2) the follicle may be completely resorbed during the beta stage leaving no histological characteristics that can be identified; and 3) the follicle may pass directly from a beta stage structure to a delta stage structure without passing through the intervening gamma stage. In northern anchovy, either the duration of the gamma stage is very short or few follicles pass through the gamma stage into the delta stage, because in regressing ovaries the incidence of gamma stages is very low compared with those of either beta or delta stages.

3) Gamma (γ) Stage Atresia—The gamma stage atretic follicle is usually much smaller than the typical beta stage follicle (Fig. 3e). The granulosa cells contain flocculent material of light-yellow hue and have nuclei of very irregular shape. The granulosa cells are surrounded by many fewer thecal cells and blood vessels than occur in the beta stage atretic follicles. Occasionally we see an atretic follicle of quite different appearance in anchovy ovaries which we classify as a gamma stage atretic follicle; they are included in the gamma stage because they also contain flocculent material of light-yellow hue. In this case, the flocculent yellow material is extracellular rather than intracellular, and the material is encapsulated by a layer of granulosa and thecal cells. It is possible that the extracellular flocculent material is produced by the disintegration of granulosa cells.

4) Delta (δ) Stage Atresia—The diagnostic characteristic of this stage is the presence of a dark yellow-brown, finely granular pigment in the granulosa cells (Fig. 3f). The delta stage atretic follicles are normally very small structures typically composed usually of 2-20 granulosa cells in the ovarian connective tissue stroma. Thecal cells and blood vessels no longer encompass the granulosa cells.

In our laboratory work 3-4 levels of abundance were recorded for each of three atretic classes seen in anchovy ovaries (alpha, beta, and gamma+delta stages). The gamma and delta stages were combined since gamma stages were rare. In addition, the alpha stage atretic class was further subdivided into three groups depending on the type of oocyte undergoing atresia (unyolked, partially yolked, and yolked oocytes). In the discussion that follows we have combined some of the abundance levels and have considered only what we believe to be the most diagnostic atretic characteristics, although all atretic characteristics as originally tabulated are given in Tables 1 and 2. The system of atretic classifications was further simplified in our presentation of the analysis of sea-caught specimens, but that will be discussed subsequently.

RESULTS

Rates of Atresia in the Laboratory

The speed at which yolked oocytes were resorbed was striking. In the first sample (elapsed time from onset of starvation = 3 d) the ovaries of 11 of the 24 females (46%) had yolked oocytes in the alpha stage of atresia (Table 1). By the 13th day, half of the females no longer had yolked oocytes, and in the rest of the females 50% or more of their yolked oocytes were in the alpha stage of oocyte

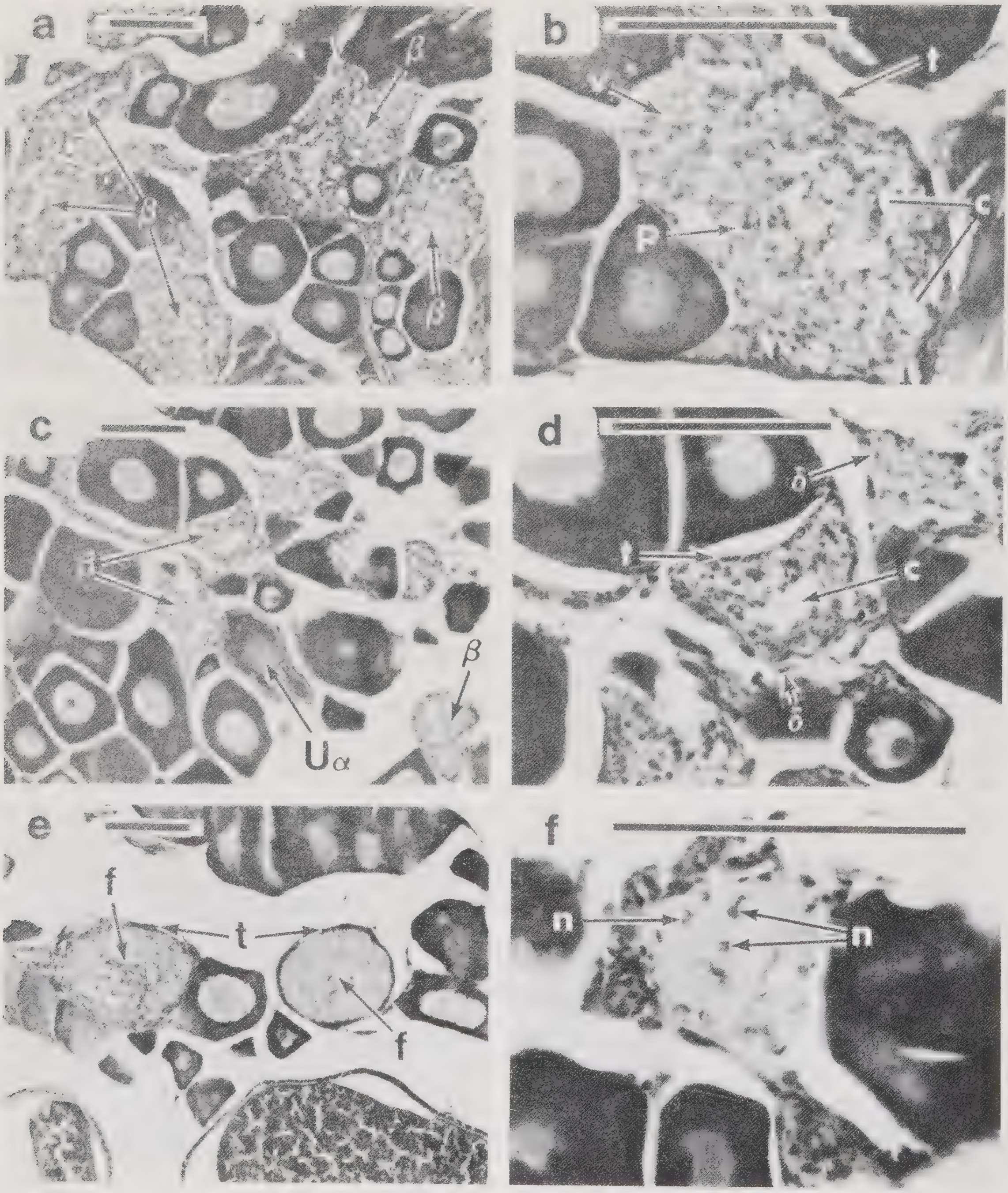

FIGURE 3.—Stages of atresia following after complete yolk absorption (bar = 0.1 mm). a) and b) Typical beta (β) stage atresia. Note the disorganized granulosa cells with some pycnotic nuclei (p) or intracellular vacuoles (v) (t = outer layer of thecal cells, c = intercellular cavities). c) and d) Disintegration of granulosa continues in these older beta (β) stage atresia. Note the large intercellular cavity (c) and the prominent, contracted thecal cell layer (t). Also present is an unyolked oocyte in early alpha (Uα) stage and several delta (δ) stage atresia cells. e) Two types of gamma (γ) atresia seen in northern anchovy ovaries. Note flocculent material (f) and the thecal layer (t). f) Delta (δ) stage atresia characterized by dark yellow fine granular pigment and an irregular nucleus (n).

TABLE 1.—Percentage of northern anchovy females with ovaries containing various levels of alpha stage atresia during starvation and after the resumption of feeding.[1]

Elapsed time from capture (d)	Feeding condition			Percentage of ovaries with levels of alpha stage atresia									
				Unyolked oocytes[2]			Partially yolked oocytes[2]			Yolked oocytes[3]			
	Starved	Fed	N	None	N <5	N >5	None	N <5	N >5	None	F < 50%	F = 50-90%	F ≥91%
3	X		24	79	13	8	46	29	25	50	33	0	13
6	X		21	19	14	67	14	14	62	5	10	19	48
9	X		24	12	17	71	0	58	34	0	8	17	42
13	X		20	10	15	75	20	15	20	0	0	5	40
16	X		24	0	12	88	4	17	17	0	0	0	8
20	X		22	0	36	64	0	0	4	0	0	0	4
23	X		23	9	39	52	0	4	13	0	0	0	0
27	X		23	4	57	39	0	0	0	0	0	0	0
34		X	23	70	17	13	4	0	0	0	0	0	0
41		X	18	83	17	0	17	0	0	17	0	0	0
62		X	22	90	5	5	64	9	9	36	23	0	0

[1] Feeding begins on the 28th day

[2] N = mean number of atretic oocytes per 6 μm section

[3] F = mean percentage of atretic oocytes per 6 μm section.

TABLE 2.—Percentage of northern anchovy females with ovaries containing various levels of beta and gamma+delta stage atresia and yolked oocytes during starvation and after the resumption of feeding.[1]

Elapsed time from capture (d)	Feeding condition			Percentage of ovaries with levels of atresia									Oocyte types	
				Beta stage atresia[2]			Beta stage atresia with no yolked oocytes[2]			Gamma + delta stage atresia[2]				
	Starved	Fed	N	None	N <5	N >5	None	N <5	N >5	None	N <5	N >5	Yolked oocytes present	Only partial and unyolked oocytes present
3	X		24	71	21	8	0	4	0	92	4	4	96	4
6	X		21	24	24	52	0	5	14	71	24	5	81	19
9	X		24	4	8	88	0	0	33	88	8	4	67	33
13	X		20	0	15	85	0	10	45	60	25	15	45	55
16	X		24	0	12	88	0	12	79	16	46	38	8	92
20	X		22	0	9	91	0	9	86	9	36	55	4	96
23	X		23	0	17	83	0	17	83	13	26	61	0	100
27	X		23	0	44	56	0	44	56	26	35	39	0	100
34		X	23	35	48	17	35	48	17	4	13	83	0	100
41		X	18	88	6	6	78	0	6	0	28	72	17	83
62		X	22	82	18	0	35	5	0	0	50	50	59	41

[1] Feeding begins on the 28th day

[2] N = mean number of atretic follicles per 6 μm section

resorption (Fig. 4). None of the females sampled on the 23d day had yolked oocytes, indicating that all yolked oocytes had passed through the alpha stage of atresia by this time.

The resorption of unyolked and partially yolked oocytes began just as rapidly as did the resorption of yolked oocytes. The percentage of females with atretic unyolked oocytes in the alpha stage increased sharply from 21% on the 3d day of starvation to 90% on the 13th day. Throughout the rest of the 27-d starvation period nearly all of the females (90-100%) had some unyolked oocytes in the alpha stage of atresia, indicating a continual recruitment of atretic follicles from the unyolked and partially yolked oocyte classes. Thus, alpha stage unyolked and partially yolked oocytes are present in regressing ovaries for a much longer period than is the alpha stage of yolked oocytes. This difference probably is due to the greater number of unyolked and partially yolked oocytes in mature ovaries. Yolked oocytes constitute <1% of the total number of oocytes present in mature ovaries.

The incidence of beta stage atretic follicles also increased sharply over the first 9 d of the starvation period and followed a pattern similar to that described for the incidence of alpha atresia from unyolked eggs (Fig. 4). After attaining a high value on the ninth day the incidence of beta atresia remained high until the end of the starvation period as atretic follicles from yolked and unyolked oocytes degraded from the alpha to the beta stage of atresia. Incidence of gamma+delta stages (the third and fourth stages of follicle degeneration) increased later than did alpha and beta stages and remained high after the onset of feeding.

Once feeding resumed (day 28), rapid resorption of yolked and unyolked follicles ceased and the

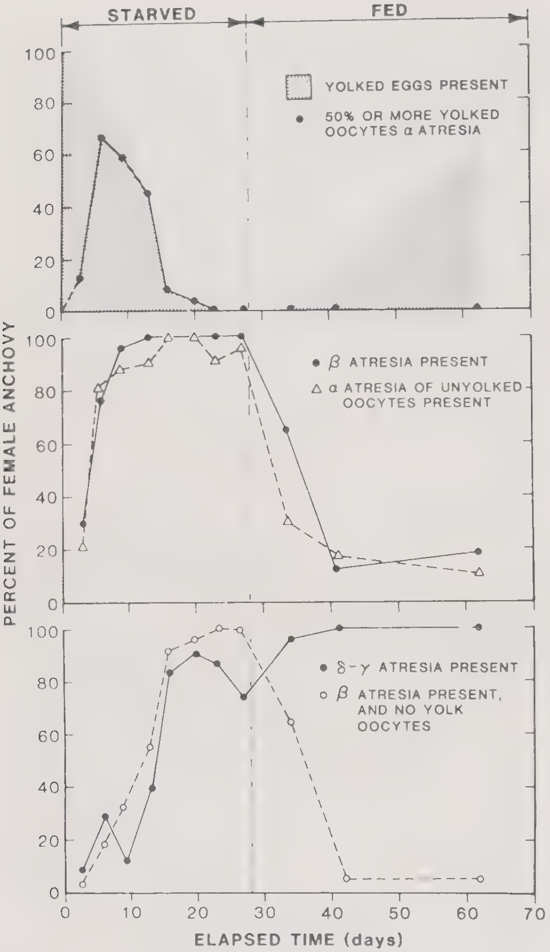

FIGURE 4.—Percentages of captive female northern anchovy with ovaries having various atretic characteristics during a 27-d starvation period and after the onset of feeding. Each percentage is calculated from a sample of 18-24 females (see Tables 1 and 2); alpha, beta, and gamma through delta stages of atretic follicles are those defined by Bretschneider and Duyvene de Wit (1941).

dominant process became maturation rather than resorption. This was indicated by sharp declines in the percentages of females with alpha stage atresia of unyolked oocytes and beta stage atretic follicles, and the reappearance of yolked oocytes (day 41). After only 1 wk of feeding the percentage of females with alpha stage atresia from partially unyolked oocytes dropped from 96 to 30%.

Some inferences can be drawn from these data regarding the duration of atretic stages. The sharp and simultaneous decline in beta stage atretic follicles and alpha stage atresia of unyolked oocytes (following the onset of feeding) indicates that alpha and beta stages must have a short and similar duration. The duration of alpha and beta atresia probably is <2 wk, since the incidence of these two stages dropped to very low levels 2 wk after the onset of feeding; a lag of about 1 wk existed between the first high incidence of females with beta atresia (9 d) and that for gamma+delta (16 d), indicating that the duration of the beta stage may be about 1 wk. The continued high incidence of gamma+delta stages of atretic follicles long after the onset of feeding indicates that these late atretic stages must persist in the ovary for much longer periods than alpha or beta stages. Although gamma+delta stages were present in all ovaries on the last day of the experiment their abundance within an ovary had decreased indicating that even the delta stage would eventually disappear, eliminating the last histological sign of past reproductive activity. We conclude from these inferences that the alpha and beta stages persist in the ovary for 1 wk or less whereas gamma+delta stages persist for over a month, but eventually all signs of past reproductive activity are lost.

The occurrence of alpha stage atresia of yolked oocytes is the best characteristic to use to back-calculate the time of past reproductive activity in field-caught specimens because the stage is of relatively short duration and the time required to resorb all yolked oocytes is relatively short. On the other hand, alpha stage atresia of unyolked oocytes, and beta and gamma+delta stages are less useful for back-calculations because these stages may occur in an ovary for extended periods while atretic oocytes are recruited from the large reservoir of unyolked oocytes in the ovary. In addition, estimates of the time since the onset of atresia in ovaries without yolked oocytes (using the incidence of beta or gamma+delta atretic stages) will always be uncertain because atresia of unyolked oocytes may occur at low levels in immature or developing ovaries as well as in regressing ovaries.

For the laboratory specimens, we calculated the average elapsed time from the onset of ovary resorption using various classes of alpha stage atresia of yolked oocytes and beta atresia in ovaries without yolked oocytes (Table 3). We prefer the criteria of 50% or more of the yolked oocytes with alpha stage atresia because it is likely that no spawning will occur in such females. The average duration of this stage (alpha, yolked, ≥50%) in the starving laboratory females was about 9 d and ranged from <3 to 20 d from the onset of starvation.

Starvation may have induced a higher rate of

TABLE 3.—Mean and maximum duration of various atretic characteristics of the ovaries of starved northern anchovy.

Atretic characteristics	Mean duration (d)	Maximum duration (d)
Alpha atresia of yolked oocytes present	8.0	20
Alpha stage atresia in:		
<50% of yolked oocytes	4.5	9
50-90% of yolked oocytes	8.1	13
91% or more of yolked oocytes	9.3	20
50% or more of yolked oocytes	9.0	20
No yolked oocytes present and beta atresia present	>16	>27

oocyte resorption than usually occurs under natural conditions. Variation in the female nutritional state, food ration, water temperature, day length, and a host of other variables may affect rates of atresia. In addition, field data indicate (see next section) that some spawning may occur in females with low to moderate levels of alpha (yolked) atresia, indicating that such stages may persist under natural conditions for extended periods. Despite these uncertainties we believe that our laboratory estimates of atretic rates are useful for making a rough estimate of the minimum time elapsed since the end of the spawning season in sea-caught females.

Natural Rates of Atresia

In this section we analyze sea data taken since 1977 for the occurrence of four ovarian atretic states in a northern anchovy population:

Atretic state 0—no alpha atresia of yolked oocytes (yolked oocytes present).

Atretic state 1—alpha atresia of yolked oocytes where <50% of the yolked oocytes are affected.

Atretic state 2—alpha atresia of yolked oocytes where 50% or more of the yolked ooctyes are affected (Fig. 5a, b).

Atretic state 3—ovaries with no yolked oocytes present and beta stage atresia present (Fig. 5c).

In addition to the atretic condition of the ovary, we also include histological evidence of recent or imminent spawning using the system of Hunter

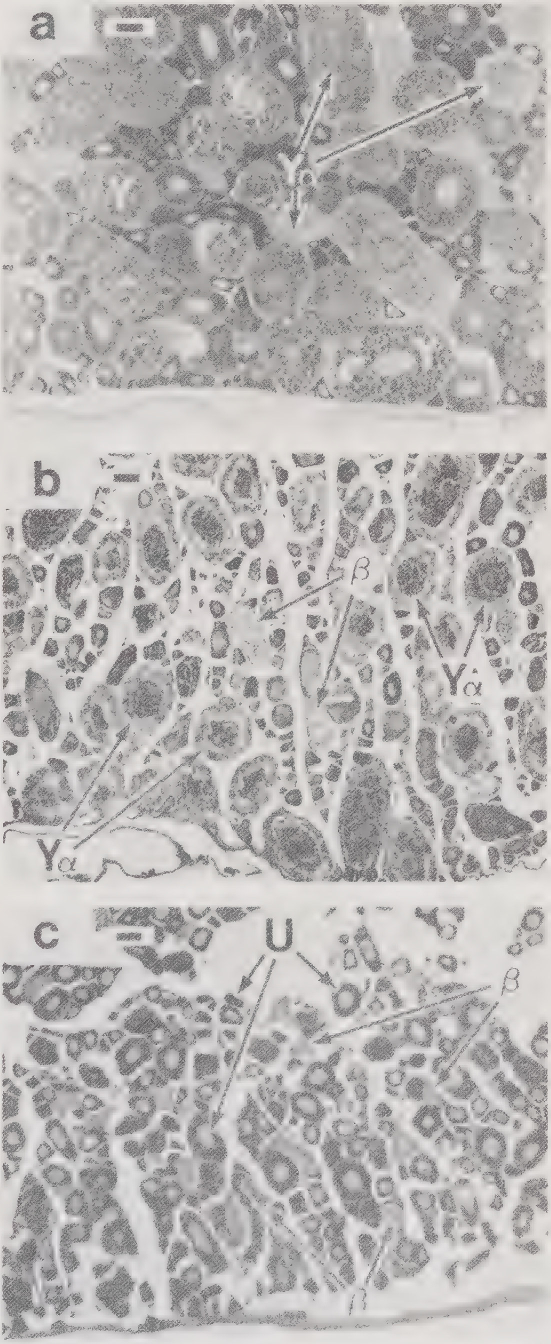

FIGURE 5.—Northern anchovy ovaries with increasing atresia states (bar = 0.1 mm). a) 50% of all yolked oocytes (Y) are in an alpha (α) stage of atresia (both early and late are counted). This is the division point between atretic state 1 and atretic state 2. b) 100% (all) yolked oocytes are in an alpha stage of atresia (Yα). Also present are a few unyolked alpha atretic oocytes and several beta (β) stage atretic follicles. This is still in atretic state 2. c) All yolk has been resorbed leaving only unyolked oocytes (U) and many beta (β) stage atretic follicles. This is atretic state 3.

and Goldberg (1980), i.e., presence of hydrated eggs (imminent spawning), day 0 or new postovulatory follicles (spawning on the night of capture), and 1-d-old postovulatory follicles (spawning on the night before capture). We also include the number of females judged to have inactive or immature ovaries with no evidence of atresia. All data on the incidence of reproductive states are given in Table 4. In the discussion that follows we select and regroup these data in various fashions to test hypotheses and document trends.

Incidence of Spawning in Atretic Females

An important assumption underlying interpretation of ovarian atresia is that the spawning season has or is going to cease, in other words, the probability of spawning in females with atretic ovaries would be expected to be low. To test this assumption we selected from Table 4 the females which had alpha stage atresia of yolked oocytes (atretic states 1 and 2) or yolked oocytes without alpha atresia (atresia state 0) and calculated the percentage of these females that had hydrated oocytes, new (day 0) postovulatory follicles, and 1-d-old postovulatory follicles. Of the females classed in atretic state 1 (females with <50% of the yolked oocytes in alpha stage of atresia), 14% showed evidence of recent or imminent spawning (postovulatory follicles or hydrated oocytes); 29% of the females without atresia showed evidence of spawning (Table 5). Only 1% of those in atretic state 2 (females 50% or more atretic yolked oocytes) had recently been reproductively active. That 1.8% of females in atretic state 1 had hydrated eggs and 3.7% had age 0 d postovulatory

TABLE 4. -Numbers of female northern anchovy in various atretic and reproductive states northern California

Collection dates number of mature females/collection	Atretic state[1]	Hydrated oocytes	Postovulatory follicles		Yolked oocytes	No yolked oocytes	Immature no histology[4]	Total
			0 day[2]	1 day[3]				
1977	0	1	2		13	4		20
09 09-09/10	1							0
	2							0
(10)	3					3		3
	x	1	2	0	13	7	0	23
1978	0				1			1
05/07-05/11	1			1	5			6
	2				4			4
(10)	3					6		6
	x	0	0	1	10	6	0	17
1979	0	39	44	52	279	89	110	613
01 26-02/16	1			1				1
	2				1			1
(10)	3					2		2
	x	39	44	53	280	91	110	617
1979	0	16	51	45	284	27	18	441
03/22-04/14	1		1	5	36			42
	2				6			6
(10)	3					16		16
	x	16	52	50	326	43	18	505
1979	0			1	8	4		13
06/09-06/19	1				3			3
	2				1			1
(12)	3					16		16
	x	0	0	1	12	20	0	33
1979	0				9	31		40
09/19-09/23	1							0
	2				5			5
(10)	3					25		25
	x	0	0	0	14	56	0	70
1980	0	25	72	52	241			390
03/20-04/10	1				9			9
	2				1			1
(20)	3					2		2
	x	25	72	52	251	2	0	402
1980	0		4	9	63	8	6	90
04 24-04/27	1				11			11
	2				14			14
(20)	3					63		63
	x	0	4	9	88	71	6	178

[1] Atretic state 0 = no alpha stage atresia of yolked oocytes.
state 1 = alpha stage atresia of yolked oocytes present but <50% oocytes affected.
state 2 = alpha stage atresia of yolked oocytes present, 50% or more oocytes affected.
state 3 = no yolked oocytes present and beta stage atresia present.

follicles indicate that some of the females in atretic state 1 spawn despite the atretic condition of their ovaries. On the other hand, only two females classed in atretic state 2 had a recent history of spawning. These two females had few yolked oocytes remaining, all but one was in alpha atresia. This atresia may have increased or even started during the time elapsed between hydration and capture. In short, the females in atretic state 2 probably did not spawn in the highly atretic state in which they were captured. No doubt exists that females with moderate levels of ovarian atresia are capable of spawning because they often are hormonally induced to do so in the laboratory. In summary these data indicate that significant numbers of females in atretic state 1 may continue to spawn under natural conditions, although the probability of spawning appears to be about half that of fish without ovarian atresia. Few or none of the females in atretic state 2 continue to spawn indicating that this stage is probably the best one to use to calculate cessation of spawning in the population.

Forcasting the end of Spawning Using Ovarian Atretic States

In our laboratory study atretic state 1 had an average duration of about 5 d and atretic state 2, 9 d; state 3 was in excess of 16 d and probably persists for 30 or more days (Table 3). In the sea, linear projections of the end of the spawning season from early incidence of atresia is not realistic since the numbers of females with regressing ovaries would be expected to increase sharply at the end of the season.

listed in order of collection dates for southern and Baja California (1977-82) and for (1979, 1982).

Collection dates number of mature females collection	Atretic state[1]	Hydrated oocytes	Postovulatory follicles		Yolked oocytes	No yolked oocytes	Immature no histology[4]	Total
			0 day[2]	1 day[3]				
1980	0			3	32	11		46
05 15-05 28	1		1		5			6
	2				2			2
(20)	3					16		16
	x	0	1	3	39	27	0	70
1981	0	119	122	148	862	58		1,309
02 05-03 06	1		2	1	19			22
	2				3			3
(15)	3					10		10
	x	119	124	149	884	68	0	1,344
1981	0	77	96	113	559	7		852
04/01-04/19	1		3	2	57			62
	2		1		45			46
(15)	3					19		19
	x	77	100	115	661	26	0	979
1981	0		2	1	7			10
04/15-04 30	1				5			5
	2				8			8
(15)	3					7		7
	x	0	2	1	20	7	0	30
1982	0	104	101	189	1,172	52	8	1,626
01/28-03/08	1	2	2	10	32			46
	2				2			2
(15)	3					6		6
	x	106	103	199	1,206	58	8	1,680
1979[5]	0		1		42			43
03/20-03/22	1		1		40			41
	2				41			41
(30)	3					25		25
	x	0	2	0	123	25	0	150
1982[5]	0	2			27	2	11	42
01/22-01/25	1	3		2	14			19
	2			1	5			6
(15)	3					13		13
	x	5	0	3	45	16	11	80

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[2] New postovulatory follicles <24 h old.

[3] Postovulatory follicles about 24 h old.

[4] Female not examined histologically, ovary ≤1% of body weight.

[5] Female northern anchovy from northern California; rest of females were from southern and Baja California.

TABLE 5.—Percentage of northern anchovy females taken from 1977 to 1982[1] that were classed in three atretic states that occurred in each of five reproductive classes.

Atretic state	Reproductive state						Total number of females
	Percent yolked oocytes with alpha stage atresia	Hydrated oocytes (%)	Postovulatory follicles		Spawning recent or imminent[2] (%)	No evidence of recent spawning[3] (%)	
			0 day (%)	1 day (%)			
0	0	7.5	9.7	12.0	29.3	70.7	5,090
1	<50	1.8	3.7	8.1	13.6	86.4	273
2	≥ 50	0	0.7	0.7	1.4	98.6	140

[1] Calculated from data given in Table 4; only females with yolked oocytes are considered

[2] Females with either hydrated oocytes or postovulatory follicles ages 0 or 1 d (the sum of the first three columns).

[3] Females with yolked oocytes but without hydrated oocytes or postovulatory follicles.

This nonlinearity becomes obvious when the end of the spawning season is extrapolated from numbers of females classed in atretic state 2. For example, of the 1,620 mature females taken during the peak of spawning (28 January-18 March 1982) in southern California (Table 4), only two were in atretic state 2 and 1,612 had yet to pass through state 2. Since laboratory data indicate that about 9 d are required to pass through atretic state 2, it would require $(1{,}612/2) \times 9$, or over 7,000 d for the entire population to become atretic at the rates of atresia observed in February, which, of course, is nonsense. Projections of the end of the spawning season using higher rates of atresia taken in April in southern California (24-27 April 1980) give a more realistic projection ($(87/14) \times 9 = 56$ d). Such an arithmetic projection may be inappropriate for collections which have a very high rate of atresia such as those taken in Monterey in March 1979 ($(84/41) \times 9 = 18$ d), and a geometric model might be preferable. The point we wish to emphasize is that atretic rates are nonlinear over the season with the rate increasing markedly as the season closes. Thus only samples taken near the close of the spawning season are of value for forecasting the end of spawning for the population.

Seasonal Changes in Atresia Among Females of Different Lengths

To evaluate how atretic rates change among females of different lengths, we segregated our data into two length classes (females ≤ 10 cm SL and those >10 cm SL) and calculated the percentage of mature females that had atretic ovaries (atretic states 1-3 combined). Mature is defined here as all females except those which have yet to reach first maturity (small females with small immature non-atretic ovaries). We also calculated the fraction of females in each length class with 1-d-old postovulatory follicles, a measure of the percentage of females spawning daily (Hunter and Goldberg 1980).

In every case, regardless of cruise or season, small females (≤ 10 cm SL) consistently had a higher rate of ovarian atresia than did larger ones (>10 cm SL) (Table 6). This is a strong trend as the probability of such an event (9 pairs of the same sign) is $(1/2)^9$. In addition, the difference between pairs was statistically significant (chi-square test) even when the levels of atresia were quite low. For example, in February-March 1981, only 4.1% of the small females and 1.9% of the large females were atretic, yet this difference was significant at $P < 0.05$ using the chi-square test. As would be expected, the percentage of females with atretic ovaries increased in both length classes as the season progressed from January through June.

The consistency of the differences in the incidence of atresia between large and small females indicates that the smaller ones must have a much shorter spawning season than larger ones. Females <10 cm long are typically about 1-yr-old and are in their first spawning season whereas those longer than 10 cm are predominantly 2-3 yr old and have spawned during the previous seasons. These data indicate that the first spawning season of females may be quite short with significant numbers of females leaving the spawning population in early April, while the older fish continue to spawn. That the rates of atresia in young fish were always higher even in the peak months of spawning such as February and March indicates that a small percentage of small females may only spawn a few times during the season in contrast to the older females which appear to be spawning at about weekly intervals for months. The fraction of small females spawning per day would be expected to be less than larger females since the small females have a higher incidence of ovarian atresia. We calculated the fraction of females spawning per

TABLE 6.—Percentage of mature northern anchovy females in two length classes with atretic ovaries. Females from north of Point Conception and groups with fewer than nine females per length class excluded.

Cruise period			Number of mature females[1]		Percent of mature females with atretic ovaries[2]		Fraction mature females spawning per day percent[3]	
From	to	year	≤10 cm	>10 cm	<10 cm	>10 cm	≤10 cm	>10 cm
01/26	→02/16	1979	121	297	1.7	0.7	8.0	15.9
01/28	→03/18	1982	97	1,523	14.6	2.6	14.1	12.2
02/05	→03/06	1981	462	824	4.1	1.9	10.2	13.7
03/20	→04/10	1980	68	334	8.8	1.8	11.7	15.2
03/22	→04/14	1979	30	430	23.3	13.3	3.8	11.8
04/01	→04/19	1981	102	870	39.2	10.0	10.5	12.9
04/24	→04/27	1980	64	100	96.9	26.0	0	8.6
04/15	→04/30	1981	10	20	80.0	60.0	0	5.3
05/15	→05/28	1980	15	44	73.3	29.5	6.2	4.4

[1] All females given in Table 4 except those with immature ovaries and those not examined histologically.
[2] All females in atretic states, 1, 2, and 3 combined.
[3] Fraction of females spawning = F, where $F = \dfrac{m_{1i}}{2m_{1i} + m_{ni}}$

m_{ni} = mature nonspawning females, and m_{1i} = females with 1-d-old postovulatory follicles.

day for the two length classes to test this assumption. We used the Stauffer and Picquelle (footnote 3) method for estimating spawning fraction as it corrects for biases in the numbers of females with hydrated eggs, i.e.,

$$F = \frac{M_{1i}}{2M_{1i} + m_{ni}}$$

where F = fraction of females spawning per day, M_{1i} = number of females with 1-d-old postovulatory follicles, and m_{ni} = number of mature females with no recent spawning history (females with postovulatory follicles or hydrated eggs are excluded). Examination of Table 6 indicates that differences in spawning fraction between the two size classes of females were much less distinct than were the differences in ovarian atresia. Using only the 8 cruises in which the numbers of females in each of the two length classes exceeded 10, the mean difference in spawning fraction (fraction for large females − fraction for small females) for the set of 8 cruises was +3.76% with 95% C.I. ±3.50% indicating a small difference in spawning frequency between the two length classes that is just barely significant at the 5% level. We believe the reason that differences in atretic fraction between large and small females are much more consistent than those in spawning fraction is that spawning fraction has a greater variability and a much more limited dynamic range than does the atretic fraction. Spawning fraction varies from 0 to about 16% and may be affected by time of day and schooling behavior (Hunter and Goldberg 1980). Atretic fraction varies from 0 to nearly 100%, is not linked to reproductive behavior, and consequently, is probably not affected by time of day or schooling.

DISCUSSION

Evaluation of Atretic Classification

Our objective was to evaluate the use of ovarian atretic states to characterize the reproductive biology of northern anchovy populations. We included in our analysis of laboratory data many atretic characteristics not used to construct the three atretic states utilized in the analysis of sea data. These additional characters could be used to create additional states or to more precisely delimit the existing ones. Our selection of characteristics was based in part on ease of identification since for population work thousands of histological sections were examined. Other considerations include the fact that statistical analysis indicated that classifiers frequently confused beta stage atretic follicles in yolked ovaries with postovulatory follicles older than 24 h, and, as a consequence, beta atresia was not used as a diagnostic character in ovaries with yolked oocytes. Alpha stage atresia was the most useful atretic stage because the type of oocyte (yolked) undergoing atresia is still discernible. In addition, alpha stage atretic oocytes can be easily distinguished from postovulatory follicles whereas this is not the case for later atretic stages.

Three atretic states were defined and applied to sea data. The incidence of all three atretic states combined was a sensitive index of the reproductive state of the population over the spawning season.

In fact, the atretic condition of the ovary was a more sensitive index of seasonal changes in the reproductive rate among size classes of females than was the incidence of spawning based on the presence of postovulatory follicles.

Atretic state 1 (<50% of yolked oocytes in the alpha stage of atresia) was not useful for estimating atretic rates in an absolute sense since this state appeared to persist in natural populations for extended and probably variable periods. Some spawning occurred among females classed in atretic state 1, although the frequency of spawning was less than half of that of females without ovarian atresia. Batch fecundity might also be reduced in females classed in atretic state 1, a speculation worth further study. Atretic state 1 was a useful index of atretic rates during peak spawning months. At such times it was the most common atretic condition and detection of differences in atretic rates among length classes was largely a function of the number of females in this state.

Atretic state 2 (50% or more of yolked oocytes in alpha atresia) persisted for about 9 d in the laboratory, and judging by its low frequency in field collections this state may have a similarly short duration in natural populations. Females with ovaries in this state rarely or never spawn, as might be expected, since more than half of the yolked oocytes are not viable. In addition, a short duration of this state also might be expected on the grounds that it seems maladaptive to prolong such a threshold condition. For the above reasons atretic state 2 seems to be the best absolute measure of the rates of ovary resorption in the population and the only state that might provide an accurate forecast of the end decline of reproduction in a population. Unfortunately, accurate forecasts of the end of spawning for a population can be made only near the end of the spawning season.

Atretic state 3 (no yolked oocytes with beta atresia present) identifies females in late postspawning condition. Such females cannot be separated from immature females on the basis of gonad weight or using gross anatomical criteria. This state persisted for about 30 d in the laboratory, but it may last much longer under natural conditions while the numerous small oocytes are resorbed. The laboratory data indicate that the duration of this state could be increased if the definitions were changed to include gamma+delta stages of atresia which have a longer life in the ovary than the beta stage. The laboratory data also indicated that even gamma+delta stages of atresia would eventually disappear from the ovary so that no signs of previous spawning activity would exist in a regressed ovary. It is doubtful that the duration of atretic state 3 or any late postspawning state will ever be accurately estimated because it is dependent on too many environmental circumstances. Nevertheless, this state is very useful in separating females in postspawning condition from females with no previous reproductive history. This is an essential distinction for estimating spawning biomass (Stauffer and Picquelle footnote 3) and for determining the size or age at first reproduction (Hunter and Macewicz 1980).

Possibly the most important future application of atretic classification of ovaries is for process oriented sea work on the reproductive biology of multiple spawning fish such as the northern anchovy. Such work does not require a large sample as do estimates of reproductive characteristics for an entire population. The reproductive state of an individual female can be accurately defined by the atretic criteria we have discussed, and the spawning state criteria described by Hunter and Goldberg (1980). The reproductive characteristics of a female can be related to its physiological state (age, fat content, biochemical composition, and instantaneous growth rate from otoliths or RNA/DNA ratios) and functional relationships established between reproduction and the environment. In this way the factors controlling the duration of the spawning season, and the total fecundity during the season, can be identified under natural conditions.

Biological Implications

Several important biological conclusions can be drawn from this work. Only a few attempts have been made to estimate the time needed for a follicle to disappear by atresia in vertebrates and no information exists for fishes (Byskov 1978). Our focus was on atretic rates of all oocytes in the ovary and not on an individual follicle; nevertheless, the striking speed with which all yolked oocytes passed through the initial stages of atresia indicate that the rate for individual follicles must be high. Similar rates were observed in the guppy by Lambert (1970a). In the guppy, alpha stage atresia of yolked oocytes appears about 1 d after parturition, and beta stage atresia appeared about 2 d after the first alpha stages were detected; beta stages persisted for only 11 d. In the anchovy, the average time for all yolked oocytes in the ovary to pass through alpha atresia was 8.0 d and the maximum time was 29 d. Thus the effect of atresia on fecundity may be underestimated since the duration of atretic stages is short and a small standing stock of atretic oocytes could be an indication of a high loss rate. On the other hand, laboratory studies seem to indicate that atretic rates are not sufficiently high to account for the differences in fecundity observed when fish are fed high and low rations (Tyler and Dunn 1976; Wootton 1979). The duration of the atretic stages in these studies was unknown, however.

Additional evidence for the volatility of the reproductive state of anchovy is an important contribution of this study. Our laboratory data indicated that given a shortage of food the ovary can be rapidly resorbed leaving no trace of former reproductive activity in a few months or less, but when given sufficient food atresia stopped, maturation and vitellogenesis resumed, and a reproductively active ovary was rapidly reformed within 35 d. Clearly, in such multiple spawning fishes as the anchovy, more than one spawning season per year is possible given the appropriate environmental conditions. This may explain the occurrence of a second annual spawning period in the Peruvian anchoveta (Santander and Castillo 1976) and the occasional heavy fall spawning of the northern anchovy (Smith 1972). That active ovaries are consistently produced from small, inactive ones in 30-60 d in the laboratory (Leong 1971; Hunter and Leong 1981) and that some reproductively active females are found the year around also supports this view.

Food shortage does not always lead to regression of the ovary in anchovy or any other multiple spawning fishes. In addition to food ration, regression of the ovary also depends upon the level of energy reserves, the timing of the reproductive cycle, and perhaps certain environmental conditions such as temperature and day length. For example, starvation of 40-80 d did not block the initial increase in the size of ovaries of the goby *Gillichthys* at the start of the reproductive cycle in July but only 23 d of starvation resulted in ovarian regression in January when active vitellogenesis was occurring (de Vlaming 1971). Similarly we noted in a preliminary experiment that starving anchovy of 25% greater wet weight than those used in this study produced a slower regression of the ovary over a 36-d period than occurred in the present study. The present study is more representative of natural conditions since the fish were taken in midspawning season when their ovaries were active whereas in the preliminary study the fish were taken out of season and fed heavily for 30 d to induce gonad maturation before the onset of the 36-d starvation period.

Another important conclusion from this study was that young female anchovy spawning for the first time probably have a much shorter reproductive season than do older females. Hunter and Leong (1981) estimated that the average female spawns about 20 times per year. Thus the older females must spawn considerably more often than 20 times per year, and probably contribute a much larger fraction of the reproductive output of the population than a proportionate share by weight. This indicates the importance of maintaining older fish in the population and that danger may exist if older fish are overharvested.

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RADIOIMMUNOASSAY RESULTS OF CIGUATERA ANALYSIS OF FISHES IN THE NORTHWESTERN HAWAIIAN ISLANDS, 1980-81

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ABSTRACT

As part of the Northwestern Hawaiian Islands (NWHI) survey and assessment investigation, tissues of various nearshore and offshore fish species were analyzed by radioimmunoassay (RIA) to evaluate the distribution of ciguatoxic fishes. From 1980 through 1981, the Honolulu Laboratory of the Southwest Fisheries Center, National Marine Fisheries Service (NMFS) sampled 43 different offshore species for a total of 1,831 tissue samples. A total of 962 samples representing 76 different nearshore species were collected by the Division of Aquatic Resources (DAR) of the Hawaii Department of Land and Natural Resources from 1980 through 1982. When analyzed by the RIA method, 2,292 (82 percent) of the samples from NMFS and DAR were negative, 278 (10 percent) were borderline, and 223 (8 percent) were positive. The results were similar to those of the 1977-79 surveys and show that commercially valuable species, especially those in the snapper-grouper complex from various NWHI locations, had moderate to high frequencies of borderline and positive RIA results. Of the nearshore species, *Cheilinus unifasciatus* (= *C. rhodochrous*) had the highest rejection rate (percentage of samples with RIA borderline and positive results). Although not previously implicated in ciguatera, *Pontinus macrocephalus* had the highest rejection rate among the offshore species, followed by *Epinephelus quernus*. Recent studies suggest that species having high rejection rates and not previously implicated in ciguatera may contain polyether compounds which are similar in chemical reactivity to ciguatoxin but of lower toxicity.

ciguatera
rejection rate
radioimmunoassay
Northwestern Hawaiian Islands

INTRODUCTION

Ciguatera is a disease caused by the ingestion of a variety of fish contaminated with ciguatoxin, a lipid originating in the dinoflagellate, *Gambierdiscus toxicus* (Yasumoto et al., 1977). Characterized by neurological and gastrointestinal symptoms, ciguatera has been a health problem as well as a deterrent to fisheries development and utilization in the oceanic islands of the Pacific.

As part of the Northwestern Hawaiian Islands survey and assessment investigation, various nearshore and offshore species of fish were sampled to determine the occurrence and distribution of ciguatoxic fishes. From 1977 until 1982, commercially important as well as other less valuable species were sampled through the cooperative efforts of the Division of Aquatic Resources (formerly the Division of Fish and Game) of the Hawaii Department of Land and Natural Resources and the Honolulu Laboratory of the Southwest Fisheries Center, National Marine Fisheries Service. Fish tissues were tested for the presence of ciguatoxin by a radioimmunoassay procedure developed at the University of Hawaii (Hokama et al., 1977).

Radioimmunoassay results of fish surveys conducted between 1977 and 1979 were reported previously (Ito and Uchida, 1980) and indicated that ciguatoxic fish occurred throughout the NWHI from Nihoa to Kure Atoll. Species among the snapper-grouper complex, including *Caranx ignobilis*, *Pseudocaranx dentex* (= *C. cheilio*), *Seriola dumerili*, *Epinephelus quernus*, *Etelis carbunculus*, *Lutjanus kasmira*, and *Pristipomoides filamentosus*, had high frequencies of borderline and positive RIA results for ciguatoxin. Among the nearshore species tested, *Kuhlia sandvicensis* and *Cheilinus unifasciatus* (= *C. rhodochrous*) had high frequencies of ciguatoxic fish.

The RIA results of nearshore and offshore surveys done from 1980 until 1982 are presented in this report. The data are similar to those of the 1977-79 surveys and show that some commercially valuable species from various NWHI locations had moderate to high frequencies of borderline and positive RIA results.

METHODS

DAR sampled fish from the nearshore areas and NMFS concentrated on sampling offshore species although some nearshore species were sampled during refueling and rest stops. Shortly after capture, each fish was weighed and measured before tissue samples were taken. Tissues collected by DAR were obtained from the anterior dorsal musculature (A); tissues collected by NMFS were taken from site A as well as from the anterior ventral abdominal musculature (B) and the posterior ventral musculature (E). Each tissue sample was placed in a plastic vial or bag and kept frozen until analyzed by the RIA method.

The RIA procedure was carried out according to the method of Hokama et al. (1977) with modifications described by Kimura et al. (1982). In the assay, precisely weighed tissue samples were incubated for 3 hours with ^{125}I - sheep anti-ciguatoxin antibody, washed, and then placed in a gamma counter to determine the radioactive counts per minute per gram of tissue. Based on studies of fish involved in clinically evaluated cases of ciguatera, and on mouse and mongoose toxicity tests, levels of toxicity were established as follows:

Counts per minute per gram	Toxicity level
<350,000	Negative
350,000 to 399,999	Borderline
>399,999	Positive

For all samples analyzed, tests were conducted "blind," i.e., samples were identified only by the original numbers assigned at the time of collection. Species identification and location of capture were revealed by NMFS and DAR only when all samples from a survey had been analyzed.

RESULTS

Approximately 18 percent of all fish sampled by NMFS and DAR showed either a positive or borderline ciguatoxin level when tested by the RIA method. Of the fish tested, 2,292 were negative, 278 were borderline, and 223 were positive.

From DAR surveys of 1980 through 1982 a total of 76 different species accounting for 962 samples were tested. Of these samples, 873 (90 percent) were negative, 53 (6 percent) were borderline, and 36 (4 percent) were positive. Table 1 shows the RIA results for the nearshore fishes and includes only those species for which a total of 10 or more samples were tested over the 3-year period. The species having the highest rejection rate (50 percent) was *C. unifasciatus* followed by *Polydactylus sexfilis* (32 percent), *Myripristis murdjan* (27 percent), *Mulloidichthys flaviolineatus* (24 percent), and *Bodianus bilunulatus* (13 percent). The rejection rates for NWHI samples in Table 1 varied from 5 percent in the summer of 1980, to 16 percent in the fall of 1980, and to 12 percent in the fall of 1981. In the summer of 1982, samples from Kure Atoll had a 2 percent rejection rate.

TABLE 1. NUMBER OF NEGATIVE (N), BORDERLINE (B), AND POSITIVE (P) REACTIONS OBTAINED WITH THE RADIOIMMUNOASSAY TEST ON FISHES CAUGHT DURING THE NORTHWESTERN HAWAIIAN ISLANDS NEARSHORE SURVEYS CONDUCTED BY THE HAWAII DIVISION OF AQUATIC RESOURCES IN 1980-82

Species*	1980 Summer	1980 Fall[†]	1981 Fall	1982 Spring-Summer[§]	Rejection[#] (%)
	N-B-P	N-B-P	N-B-P	N-B-P	
Acanthurus nigroris	--	--	2-0-0	9-0-0	0
A. triostegus	45-1-3	17-3-0	48-0-2	25-0-0	6
Bodianus bilunulatus	12-1-2	14-5-1	34-0-0	2-0-0	13
Carangoides ferdau	--	--	10-0-0	1-0-0	0
Caranx ignobilis	10-0-0	1-0-0	4-0-0	1-0-0	0
C. melampygus	5-0-0	4-0-0	5-1-1	--	12
Cheilinus unifasciatus	--	2-4-1	4-0-1	--	50
Kuhlia sandvicensis	51-1-0	19-0-0	38-5-0	37-2-0	5
Kyphosus bigibbus	22-0-0	13-3-2	--	25-0-0	8
Mulloidichthys flaviolineatus	1-0-0	10-6-1	11-0-0	--	24
Myripristis amaenus	14-1-1	--	8-0-0	10-0-0	6
M. murdjan	--	6-0-1	10-2-3	--	27
Parupeneus multifasciatus	--	--	13-1-0	--	7
P. porphyreus	5-0-0	27-1-1	3-1-2	1-0-0	12
Priacanthus sp.	--	7-0-0	--	7-0-0	0
Polydactylus sexfilis	--	--	19-1-8	--	32
Pseudocaranx dentex	--	13-0-0	--	1-0-0	0
Thalassoma duperreyi	--	19-1-0	--	--	5
Selar crumenophthalmus	30-0-0	--	--	--	0
TOTAL	195-4-6	153-23-7	209-11-17	119-2-0	

*Only species of which 10 or more samples were collected are included.

[†] Fishes were collected only from Midway and Kure Atoll.

[§] Fishes were collected only from Kure Atoll.

[#] Percent rejection = number borderline + positive fish/total number tested x 100.

From the NMFS surveys of 1980 through 1981, a total of 43 different species accounting for 1,831 samples were tested. Of these samples, 1,419 (78 percent) were negative, 225 (12 percent) were borderline, and 187 (10 percent) were positive. Table 2 shows the RIA results for species that had a sample size of at least 10 during this period. Although only 16 samples of *Pontinus macrocephalus* were analyzed from 6 locations, this species had a rejection rate of 50 percent, the highest among all species examined. *Epinephelus quernus*, the only serranid sampled, had the next highest rejection rate of 39 percent, based upon 308 fish from 19 locations. Among the carangids, *Pseudocaranx dentex* had the highest rejection rate (22 percent), followed by *Caranx ignobilis* (18 percent) and *Seriola dumerili* (10 percent). Among the snappers, *Pristipomoides zonatus* had a rejection rate of 36 percent, followed by *P. filamentosus* (26 percent), *Etelis carbunculus* (22 percent), and *P. sieboldii* (10 percent). Samples collected only from Midway gave moderate to high rejection rates: *Acanthurus triostegus* (25 percent), *Selar crumenophthalmus* (14 percent), and *K. sandvicensis* (10 percent).

For the NMFS surveys, comparison of rejection rates according to locations of capture indicates that Lisianski (44 percent) and Raita Bank (43 percent) had the highest rates of rejection. The following locations also showed high rates of rejection: Kure Atoll (33 percent), Laysan Island (28 percent), Pearl and Hermes Atoll (27 percent), French Frigate Shoals (26 percent), Maro Reef (23 percent), Necker Island (23 percent), Nihoa (21 percent), and Gardner Pinnacles (17 percent).

DISCUSSIONS AND CONCLUSIONS

The results of the NMFS and DAR surveys for ciguatoxic fish during 1980 through 1982 are similar to those obtained in the 1977-79 surveys (Ito and Uchida, 1980). Fish having borderline or positive RIA results were found among many of the species examined and appeared to be distributed throughout the NWHI. The results are in agreement with those of Sylvester et al. (1977) who reported that members of the family Carangidae, followed by snappers and groupers, were the species most likely to be ciguatoxic in the Virgin Islands.

A comparison of the data obtained by DAR and NMFS shows that higher rejection rates were found in the NMFS surveys: 22 percent vs 9 percent. A possible explanation for the difference is that the DAR rejection rates were based on only one tissue sampling site (A) for each fish whereas the NMFS rejection rates were based on results from three tissue sites (A, B, and E). No consistent relationship has been found between toxicity as determined by the RIA method and tissue sampling site. Therefore, the higher rejection rates for the NMFS samples may have resulted from the greater chance of detecting ciguatoxin since tissues from three sites rather than one were tested.

TABLE 2. NUMBER OF NEGATIVE (N), BORDERLINE (B), AND POSITIVE (P) REACTIONS OBTAINED WITH THE RADIOIMMUNOASSAY ATEST ON FISHES CAUGHT DURING THE NATIONAL MARINE FISHERIES SERVICE SURVEY CRUISES TO THE NORTHWESTERN HAWAIIAN ISLANDS IN 1980-81

Species	Nihoa	Twin Banks	Necker	French Frigate Shoals	Brooks Banks	St. Rogatien	Gardner Pinnacles	Raita Bank
	N-B-P	N-B-P	N-B-P	N-B-P	N-B-P	N-B-P	N-B-P	N-B-P
Acanthuridae								
Acanthurus triostegus								
Carangidae								
Caranx ignobilis			0-0-1	1-1-0			1-0-0	
Pseudocaranx dentex	1-0-0		8-3-2	9-3-3		12-0-0	22-2-2	11-4-0
Seriola dumerili	3-0-0	4-0-0	15-1-0	12-0-0	1-0-0	3-0-0	21-5-1	12-1-0
Selar crumenophthalmus								
Kuhliidae								
Kuhlia sandvicensis								
Kyphosidae								
Kyphosus bigibbus								
Lutjanidae								
Etelis coruscans		1-0-0				1-0-0	4-0-0	
E. carbunculus	2-0-0	2-0-0	13-3-4	6-2-2		8-2-0	9-0-2	2-0-0
Pristipomoides filamentosus	1-0-0		59-10-8	48-7-6	2-0-0	11-3-1	15-2-0	3-6-3
P. sieboldii	0-1-0	2-0-0	8-0-0	1-1-0		2-0-0	2-0-0	1-0-1
P. zonatus			3-1-0	1-3-0			4-0-0	1-0-0
Mullidae								
Mulloidichthys flaviolineatus								
Priacanthidae								
Priacanthus meeki								
Scombridae								
Acanthocybium solandri	1-0-0		8-0-0		1-0-0		1-0-0	2-0-0
Euthynnus affinis	2-0-1		12-0-0			1-0-0		
Scorpaenidae								
Pontinus macrocephalus								
Serranidae								
Epinephelus quernus	1-1-0	3-0-0	9-6-2	25-5-3		13-1-0	11-1-1	9-8-8
TOTAL	11-2-1	12-0-0	135-24-17	103-22-14	4-0-0	51-6-1	90-10-6	41-19-12

TABLE 2. NUMBER OF NEGATIVE (N), BORDERLINE (B), AND POSITIVE (P) REACTIONS OBTAINED WITH THE RADIOIMMUNOASSAY TEST ON FISHES CAUGHT DURING THE NATIONAL MARINE FISHERIES SERVICE SURVEY CRUISES TO THE NORTHWESTERN HAWAIIAN ISLANDS IN 1980-81 (continued)

Species	Maro Reef	Laysan	Northampton Seamount	Lisianski	Bank No. 9	Pearl and Hermes Reef	Grass	Salmon Bank
	N-B-P	N-B-P	N-B-P	N-B-P	N-B-P	N-B-P	N-B-P	N-B-P
Acanthuridae								
Acanthurus triostegus								
Carangidae								
Caranx ignobilis	2-0-0			2-1-0		25-4-0		
Pseudocaranx dentex	3-1-1	13-2-2		2-0-0	1-0-1	33-4-2		
Seriola dumerili	11-0-0	12-3-0		3-0-0	3-1-0	13-0-0		
Selar crumenophthalmus								
Kuhliidae								
Kuhlia sandvicensis								
Kyphosidae								
Kyphosus bigibbus								
Lutjanidae								
Etelis coruscans		1-0-0			1-0-0	4-0-0		
E. carbunculus	4-0-1	23-3-6	11-0-2		13-1-0	90-14-18	4-0-0	26-1-0
Pristipomoides filamentosus	7-4-0	3-1-0	1-0-0	1-1-0	1-0-0	2-0-0		
P. sieboldii		8-0-0	1-0-0		2-0-0	6-0-0	2-0-0	6-0-0
P. zonatus	2-0-0	8-0-4	5-0-0		1-0-0	2-1-1		1-0-0
Mullidae								
Mulloidichthys flaviolineatus								
Priacanthidae								
Priacanthus meeki								
Scombridae								
Acanthocybium solandri	3-0-0	1-0-0						
Euthynnus affinis		4-1-0		0-1-0				
Scorpaenidae								
Pontinus macrocephalus		0-0-1		2-0-1		2-2-2		1-0-0
Serranidae								
Epinephelus quernus	8-4-1	27-12-0	3-0-0	5-4-4	13-3-1	39-10-23		1-1-0
TOTAL	40-9-3	97-22-13	21-0-2	15-7-5	35-5-2	216-35-46	6-0-0	35-2-0

TABLE 2. NUMBER OF NEGATIVE (N), BORDERLINE (B), AND POSITIVE (P) REACTIONS OBTAINED WITH THE RADIOIMMUNOASSAY TEST ON FISHES CAUGHT DURING THE NATIONAL MARINE FISHERIES SERVICE SURVEY CRUISES TO THE NORTHWESTERN HAWAIIAN ISLANDS IN 1980-81 (continued)

Species	Ladd Bank	Midway	Eastern	Nero and Pogy	Kure Atoll	Bank No. 11	Total All Banks	Rejection (%)
	N-B-P	N-B-P	N-B-P	N-B-P	N-B-P	N-B-P	N-B-P	
Acanthuridae								
Acanthurus triostegus		51-10-8	2-0-0				53-10-8	25
Carangidae								
Caranx ignobilis		1-0-0					32-6-1	18
Pseudocaranx dentex	2-1-0	1-0-0		1-0-0	2-1-0		121-21-13	22
Seriola dumerili		0-1-0	1-0-0	3-0-0			117-12-1	10
Selar crumenophthalmus		24-3-1					24-3-1	14
Kuhliidae								
Kuhlia sandvicensis		223-14-11					223-14-11	10
Kyphosidae								
Kyphosus bigibbus		19-0-0					19-0-0	0
Lutjanidae								
Etelis coruscans							12-0-0	0
E. carbunculus	17-3-4	1-0-0		12-1-2	9-1-0		252-31-41	22
Pristipomoides filamentosus				0-1-1			154-35-19	26
P. sieboldii	2-2-0			1-0-0	1-0-0		45-4-1	10
P. zonatus							28-5-5	36
Mullidae								
Mulloidichthys flaviolineatus		13-0-0					13-0-0	0
Priacanthidae								
Priacanthus meeki		12-1-1					12-1-1	14
Scombridae								
Acanthocybium solandri					1-0-0		18-0-0	0
Euthynnus affinis					0-0-1		19-2-2	17
Scorpaenidae								
Pontinus macrocephalus				1-0-0	2-2-0		8-4-4	50
Serranidae								
Epinephelus quernus	7-0-6	1-0-0		5-1-4	7-5-1	1-2-2	188-64-56	39
TOTAL	28-6-10	346-29-21	3-0-0	23-3-7	22-9-2	1-2-2		

Similar to the results of earlier surveys, the nearshore species showing the highest rejection rate was *Cheilinus unifasciatus* which has been frequently implicated in ciguatera. Of the offshore species *Pontinus macrocephalus* had the highest rejection rate. However, this species has not been implicated in ciguatera in the past. Another offshore species having a high rejection rate was *Epinephelus quernus*, a member of the grouper family which has been implicated in ciguatera.

Results of surveys from 1977 through 1982 indicate that certain species (such as *P. macrocephalus* and *Pristipomoides* sp.), which have not been implicated in ciguatera, have high rejection rates based on the RIA. Recent studies describing the existence of compounds with structures similar to ciguatoxin suggested the possibility that the sheep anti-ciguatoxin antibody may also react with these compounds. Tachibana et al. (1981) reported that two marine sponges (genus *Halichondria*) contained okadaic acid, a cytotoxic polyether compound having close structural similarity to ciguatoxin. Murakami et al. (1982) identified okadaic acid as the toxic component in *Prorocentrum lima*, a benthic marine dinoflagellate, and found close similarity between okadaic acid and ciguatoxin in terms of chromatographic and ionophoric properties, and oxygenated polyether structure. Another marine toxin, brevetoxin B, from the red tide dinoflagellate *Ptychodiscus brevis*, also has a polyether structure similar to ciguatoxin (Lin et al., 1981).

Preliminary studies indicate that purified okadaic acid and brevetoxin partially inhibit the binding of sheep anti-ciguatoxin to toxic fish tissues, although at concentrations greater than those required for similar inhibition by purified ciguatoxin (unpublished observations). The presence of these ciguatoxinlike compounds in fish tissues may give positive RIA results and yet may not cause toxic symptoms because they are inherently less toxic than ciguatoxin. The LD_{99} of highly purified ciguatoxin is 0.45 μg/kg when given intraperitoneally to mice (Tachibana, 1980) whereas the LD_{99} of okadaic acid is 200 μg/kg (Murakami et al., 1982) and that of brevetoxin T34 is between 150 and 270 μg/kg (Baden et al., 1981).

In conclusion, results of the DAR and NMFS surveys of the nearshore and offshore waters of the NWHI indicate that approximately 18 percent of the fishes examined gave borderline or positive results by the RIA method. Offshore species that belong to the snapper-grouper complex showed a high degree of rejection. Among nearshore species, *C. unifasciatus* showed high rejection rates. More recent studies suggest that species with high rejection rates but not previously implicated in ciguatera may contain polyether compounds similar to ciguatoxin but of lower toxicity. Further studies are needed to examine this possibility, especially in view of the recent availability of techniques to develop monoclonal antibodies which could be used instead of the polyclonal sheep anti-ciguatoxin.

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Thermal dependence of contractile properties of single skinned muscle fibres from Antarctic and various warm water marine fishes including Skipjack Tuna (*Katsuwonus pelamis*) and Kawakawa (*Euthynnus affinis*)

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Summary. Single fast fibres and small bundles of low fibres were isolated from the trunk muscles of an Antarctic (*Notothenia neglecta*) and various warm water marine fishes (Blue Crevally, *Carangus melampygus*; Grey Mullet, *Mugil cephalus;* Dolphin Fish, *Coryphaena hippurus;* Skipjack-tuna, *Katsuwonus pelamis* and Kawakawa, *Euthynuus affinis*). Fibres were chemically skinned with the non-onic detergent Brij 58.

For warm water species, maximum Ca^{2+}-activated tension (P_0) almost doubled between –20 °C with little further increase up to 30 °C. However, when measured at their normal body emperatures, P_0 values for fast fibres were similar or all species examined, 15.7–22.5 $N \cdot cm^{-2}$. Ca^{2+}-egulation of contraction was disrupted at temperatures above 15 °C in the Antarctic species, but was maintained at up to 30 °C for warm water fish.

Unloaded (maximum) contraction speeds (V_{max}) of fibres were determined by the "slackest" method. In general, V_{max} was approximately wo times higher in white than red muscles for ll species studied, except Skipjack tuna. For Skipack tuna, V_{max} of superficial red and white fibres was similar (15.7 muscle lengths$\cdot s^{-1}$ ($L_0 \cdot s^{-1}$)) but were 6.5 times faster than the V_{max} of internal red muscle fibres (2.4 ± 0.2 $L_0 \cdot s^{-1}$) (25 °C).

V_{max} for *N. neglecta* fast fibres at 0–5 °C 2–3 $L_0 \cdot s^{-1}$) were similar to that of warm water pecies measured at 10–20 °C. However, when measured at their normal muscle temperatures, the V_{max} for the fast muscle fibres of the warm water pecies were 2–3 times higher than that for *N. neglecta*.

In general, $Q_{10(15-30\,°C)}$ values for V_{max} were in the range 1.8–2.0 for all warm water species studied except Skipjack tuna. V_{max} for the internal red muscle fibres of Skipjack tuna were much more temperature dependent ($Q_{10(15-30\,°C)}=3.1$) ($P<0.01$) than for superficial red or white muscle fibres. The proportion of slower red muscle fibres in tuna (28% for 1 kg Skipjack) is 3–10 times higher than for most teleosts and is related to the tuna's need to sustain high cruising speeds. We suggest that the 8–10 °C temperature gradient that can exist in Skipjack tuna between internal red and white muscles allows both fibre types to contract at the same speed. Therefore, in tuna, both red and white muscle may contribute to power generation during high speed swimming.

Introduction

Myosins from cold-water fish are unstable and susceptible to aggregation on isolation compared to those prepared from tropical species (Connell 1961; Johnston et al. 1974). The greater susceptibility of myosin ATPase from Antarctic fish to thermal denaturation has been correlated with an increased enzyme activity at low temperatures and reduced free energy of activation relative to myosin ATPase from warmer water species (Johnston and Walesby 1977, 1979). Previous studies of temperature compensation of contraction have dealt with the properties of isolated proteins in solution (see Clarke 1983, for a review). The extent to which the mechanical properties of muscles of animals from widely different thermal environments are similar is unknown. There is evidence to suggest that the thermal dependence of biochemical systems in vitro does not reflect that of more highly organised systems in vivo. For example, MgCa-ATPase activity of Sculpin (*Myoxocephalus scorpius*) fast muscle myofibrils increases 8-fold between 0.5 and 20 °C, compared with an increase of only 2.5-fold for unloaded (maximum) contraction speed ($V_{\max}$) (Johnston and Sidell 1984).

The present study was undertaken to examine the thermal dependence of muscle contraction speeds at the two extremes of body temperature found among fishes. Notothenioid fishes are restricted to South Polar seas (DeWitt 1971), and have a number of adaptations, such as glycoprotein antifreeze molecules, which enable them to live at sub-zero temperatures (Clarke 1983). At the other extreme, tuna species are highly specialised tropical and sub-tropical scrombroids that are able to maintain elevated red muscle temperatures which are especially dramatic during periods of high speed swimming.

Elevated muscle temperatures are achieved using retia mirabilia as counter current heat exchangers to conserve metabolic heat (Carey and Teal 1969; Stevens and Neill 1978). Stevens and Neill (1978) have reported that for Skipjack tuna, aerobic metabolism can produce internal red muscle temperatures 10 °C above ambient water temperatures during periods of burst swimming.

Tuna have substantially higher metabolic rates than other fish (Stevens and Neill 1978) and a number of special adaptations for high speed swimming including the adoption of ram ventilation and various morphological features to reduce drag, such as caudal peduncle finlets, eye fairings, and slots for the dorsal fins (Magnuson 1978; Sharp and Pirages 1978). Therefore, a second objective of this study was to determine if adaptations for high speed swimming were also reflected in higher muscle contraction velocities.

Materials and methods

Fish. Notothenia neglecta (Nybelin) (500–700 g) were obtained from Signy Island, South Orkneys, British Antarctic Territories (Lat. 60°43′S Lon. 45°36′W) during Austral summer, 1982. They were transported to the U.K. aboard the R.R.S. Bransfield and maintained at St Andrews in filtered seawater tanks at +2 °C. *Notothenia* were fed a diet of chopped squid and fish flesh. The remaining species studied were caught by commercial fishermen around the Hawaiian Island of Oahu. Fish were maintained at the National Marine Fisheries Service, Honolulu, Hawaii, (USA) Kewalo Research Facility in outdoor 6 m diameter circular tanks with direct flow-through sea-water supply. Water temperature was that of ambient surface seawater for June-July, 24–28 °C. All fish were fed a diet of sprats and chopped squid. Species studied were Skipjack tuna (*Katsuwonus pelamis*, 8 fish, 1.2 ± 0.2 kg, 39.8 ± 0.4 cm); Kawakawa (*Euthynnus affinis*, 5 fish, 3.2 ± 0.4 kg, 51.2 ± 1.1 cm); Dolphin fish (*Coryphaena hippurus*, 1 fish, 11 kg, 120 cm); Grey mullet (*Mugil cephalus* L., 6 fish, 1,137 ± 164 g, 41 ± 2 cm) and Blue Crevally (*Carangus melampygus* Wakiya, 5 fish, 304 ± 21 g, 25 ± 1 cm).

Choice of preparation. Both fast and slow muscle fibres are polyneuronally innervated in most teleosts often with as many as 15–20 motor-endplates per fibre (Bone 1978; Johnston 1983a, b). Dissection of small fibre bundles inevitably results in a variable proportion of damaged and inexcitable fibres. Such preparations produce relatively low tetanic tensions on electrical stimulation (Flitney and Johnston 1979). Single skinned fibre preparations from fish produce much higher maximum tensions in the range reported for skinned preparations from other vertebrate muscles (Altringham and Johnston 1982). For frog fibres, maximum isometric tensions are somewhat lower for skinned than intact preparations, whereas maximum contraction velocities are similar (Julian 1971; Edman and Hwang 1977). Skinned fibres have therefore been chosen as the most suitable preparation for comparative studies of muscle mechanics in fish.

Experimental protocol. Fish were stunned by a blow to the head and pithed. Strips of red and white muscle were dissected from 2–3 myomeres half way along the length of the trunk. In the case of the tuna species, both superficial and internal deep red muscle were sampled (Fig. 1). Subsequent dissection was carried out under silicon oil (BDH MS 550) in a 2 mm deep glass trough. Single red and white fibres were isolated from a 20–30 fibre bundle dissected from a single myotome. Fibre lengths in the region sampled were 1.8 cm for Grey mullet and 0.8–1.0 cm for all other species studied. Single fibre segments, 90–100 µm diameter and 1.3–3.2 mm length, were transferred directly to the apparatus using jewellers' forceps. A thin coating of oil remained on each fibre and helped prevent dehydration during the 15–30 s required to transfer and mount fibres.

Measurement of contractile properties. Muscle fibres were mounted with the aid of a binocular microscope and then chemically skinned with 1% Brij 58 (polyoxyethylene 20-cetyl ether) dissolved in relaxing solution. Relaxing solution contained 20 mM imidazole – HCl, 110 mM KCl, 3.0 mM $MgCl_2$, 5 mM EGTA (ethyleneglycolbis β-aminoethylether N,N′-tetraacetic acid), 10 mM phosphocreatine, 2.5 mM ATP, pH 7.2 at 20 °C. Crystalline creatine phosphokinase (>20 units·ml^{-1}, Sigma Chemical Co, Poole, England) was added to all incubation solutions just prior to experiments. In all experiments, pH was allowed to vary freely with temperature. Imidazole was chosen as the buffer since it has a $\Delta pH/\Delta T$ curve similar to that reported for blood and tissue from many fish species (Reeves 1977). Activating solutions were prepared by addition of a 1 M volumetric solution of $CaCl_2$ to yield a final concentration of 4.0–5.0 mM. Ionic compositions were determined using an iterative computer programme written in BBC Basic, based on that described by Fabiato and Fabiato (1979). The programme was modified to correct for changes in ionic composition with alterations in temperature and pH (stability constant CaEGTA Ca. EGTA $= 8.89 \times 10^{10}$ at 22 °C). Total ionic strength of the activating solution was 0.17 M, free concentrations of Ca^{2+}, Mg^{2+} and MgATP were 5–15 µM, 0.50–0.54 mM and 2.31–2.52 mM, respectively. Ca^{2+}-concentrations required to give maximally activated concentrations at each temperature were determined in a series of preliminary experiments.

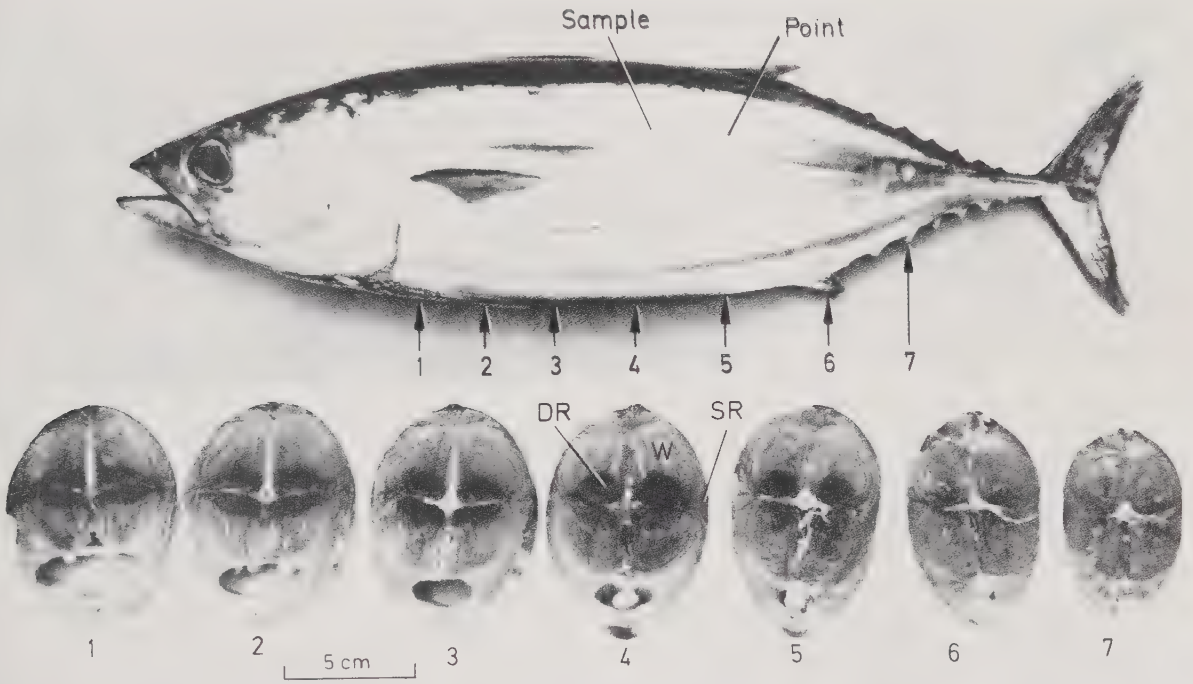

Fig. 1. Sample points for isolation of the different muscle fibre types in Skipjack tuna (*Katsuwonus pelamis*): *SR* superficial red muscle; *DR* deep internalised red muscle; *W* white muscle. Deep red muscle has a much higher myoglobin concentration than superficial red muscle

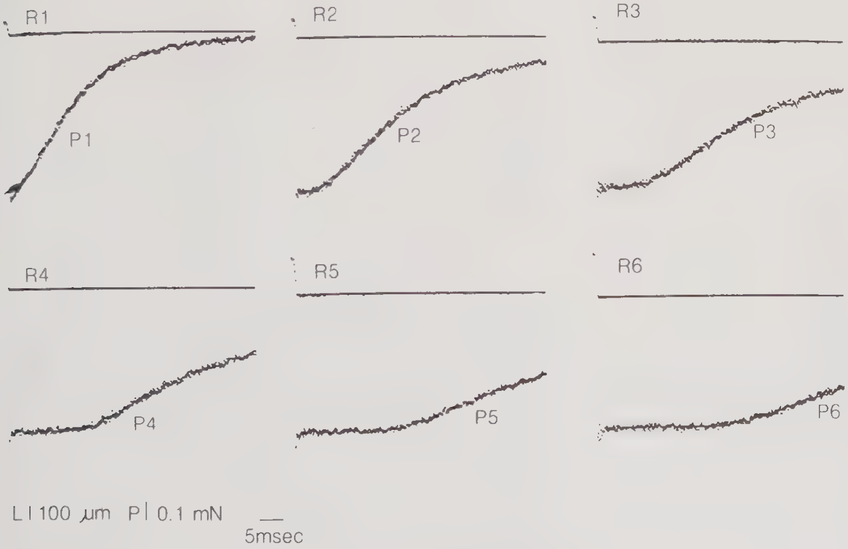

Fig. 2. A typical series of records (R1–R6) illustrating the 'slack-test' method for determining unloaded contraction velocity. White fibre segment, 2,300 µm in length and 90 µm in diameter, isolated from Skipjack tuna muscle. P indicates tension and L muscle length. Note the direction of shortening is down and tension redevelopment is up

Unloaded contraction velocity (V_{max}) was determined by the slack test method (Hill 1970). The apparatus and experimental protocol used have been described in detail elsewhere (Johnston and Sidell 1984; Johnston and Gleeson 1984). Force was measured using a silicon beam tension transducer (Akers AE801, AME, Horton, Norway) attached via a small glass hook to one end of the fibre. The other end of the fibre was attached to a second hook glued to a servo-controlled length transducer (Johnston and Sidell 1984). Fibres were attached to the glass hooks using plexiglass acetone glue (Altringham and Johnston 1982). In a typical experiment, fibres were transferred sequentially to baths containing skinning solution, relaxing solution, activating solution and relaxing solution. The baths were water-jacketed and temperature control (in the range of 0–30 °C) was maintained using a circulating constant temperature water bath (±0.1 °C). The sarcomere length of fibres was determined prior to releases by laser diffraction using a 2 mW Helium-Neon laser and adjusted to 2.3 µm. Once steady

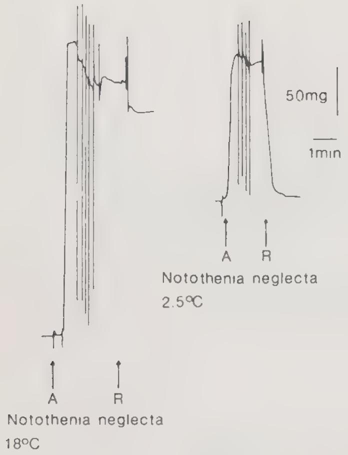

Fig. 3. Records showing isometric contractions of white fibres isolated from *Notothenia neglecta* at 2.5 °C and 18 °C. Arrows indicate transfer from relaxing to activating solutions (*A*) and vice versa (*R*). Fibres from Antarctic fish failed to relax following transfer from activating to relaxing solution at temperatures above 14–15 °C

Table 1. Maximum Ca^{2+}-activated tension (P_0) generation by red and white myotomal muscle fibres of fish measured at their normal body temperature. Means ±SEM, numbers of fibres used in brackets

Species and environmental temperature range	Temperature (°C)	Maximal Ca^{2+}-activated force ($N \cdot cm^{-2}$)	
		Red fibres	White fibres
Notothenia neglecta Antarctica (−2 to +1 °C)	0	–	22.5±2.2 (6)
Gadus morhua[a] (North Sea, 2–15 °C)	8	8.3±1.0 (11)	18.7±1.8 (13)
Mugil cephalus (Pacific reefs, 20–28 °C)	20	5.2±0.6 (11)	21.0±2.8 (8)
Carangus melampygus (Pacific reefs, 20–28 °C)	25	4.3±0.6 (4)	18.3±1.7 (6)
Katsuwonus pelamis[b] (Pacific, open ocean, 15–28 °C)	25	2.4±0.2 (6)	15.7±1.3 (11)
Euthynnus affinis[b] (Pacific, open ocean, 15–28 °C)	30	2.5±0.3 (10)	18.8±0.8 (6)

[a] Data from Altringham and Johnston (1982)

[b] Values are from deep-red muscle for the tuna species

tension was developed on transference to activating solution (30–60 s), a series of quick releases (≦1 ms) of sufficient magnitude to abolish tension, were given. Usually 4 or 5 lengthsteps of increasing magnitude (50–250 μm) were imposed on the fibre during each series of releases. Transients were recorded on a storage oscilloscope. Between each release (ΔL) fibres were re-extended to their original length. Unloaded contraction velocity (V_{max}) was determined from an average of the time taken to redevelop tension (Δt) following each release. A typical record illustrating the method of determining V_{max} is shown in Fig. 2. Muscle length and diameter were measured in situ using a high power microscope.

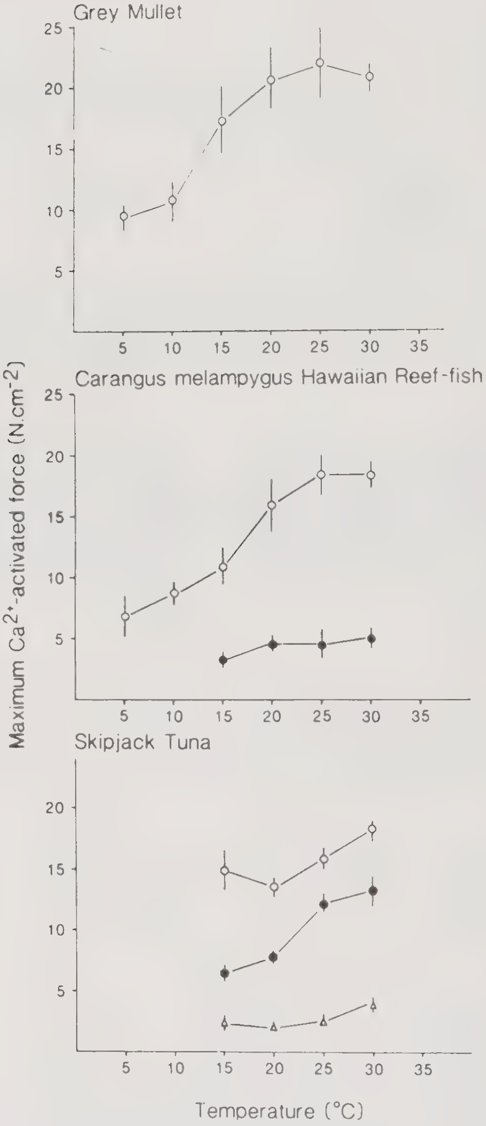

Fig. 4. Effect of temperature on maximum Ca^{2+}-activated force generation of muscle fibres isolated from (top) Grey mullet (white fibres), (centre) Blue Crevally (open circles, white fibres; closed circles, superficial red fibres) and (bottom) Skipjack tuna (open circles, white fibres; closed circles, superficial red fibres; open triangles deep internal red muscle fibres)

Results

At an initial sarcomere length of 2.3 μm, skinned muscle fibres from the warm water species showed

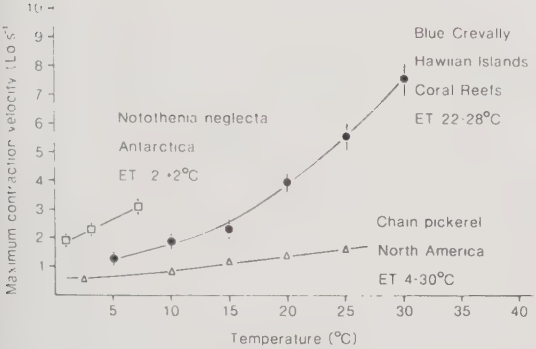

Fig. 5. Effect of temperature on unloaded contraction velocity of skinned fibres isolated from fish white muscle. Data on Chain Pickeral *Esox niger* is taken from Sidell and Johnston (submitted for publication). *ET* indicates the species' thermal habitat

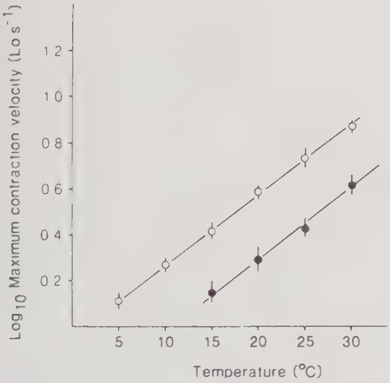

Fig. 6. Effect of temperature on unloaded contraction velocity of red (closed circles) and white (open circles) muscle fibres isolated from the Blue Crevally. The plot shows $\log_{10} V_{\max}$ (muscle length$\cdot$s^{-1}) versus temperature

no development of resting tension and complete relaxation of tension following activation for temperatures up to 30 °C. In contrast, fast fibres isolated from *Notothenia neglecta* failed to relax completely following activations above 15 °C (Fig. 3). At temperatures above 22 °C, *N. neglecta* fibres contracted in relaxing solution (pCa 7.4) and contractions were independent of Ca^{2+} concentrations.

For all species studied, maximal Ca^{2+}-activated tensions (P_0) were 2–3 times higher for white than superficial red fibres. This difference is somewhat greater than can be accounted for by the higher relative volume densities of myofibrils in white than red fibres (Johnston 1981). P_0 for the internal deep red muscle of the two tuna species was only 15% that of white fibres and less than that for the superficial red muscle of any other species (Table 1). In spite of a 30 °C difference in temperature, P_0 of white fibres were similar when measured at the normal body temperature of each species (15.7–22.5 N$\cdot$cm^{-2}: Table 1). For warm water species, P_0 almost doubled between 5–20 °C with little further increase over the range 20–30 °C (Fig. 4).

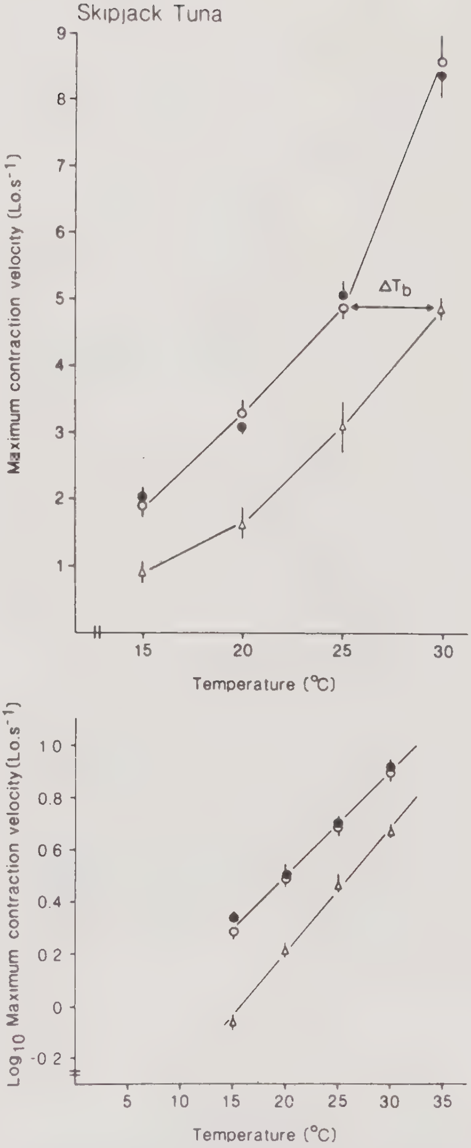

Fig. 7. Effect of temperature on unloaded contraction velocity of superficial red (closed circles), deep, internalised red (open triangles) and white muscle fibres (open circles) isolated from the Skipjack tuna. ΔT_b shows the maximum temperature gradient between internal red and white muscle reported by Stevens and Neill (1978). Note similar contraction speeds for red and white muscle fibres for an 8–12 °C temperature difference. A $\log L_0\cdot s^{-1}$ vs T plot gives straight lines in each case

Table 2. Thermal dependence of unloaded contraction velocity for red and white muscles isolated from tropical marine fish. Means ±SEM (n)

Species	Muscle type	V_{max}, 20 °C ($L_0 \cdot s^{-1}$)	V_{max}, 30 °C ($L_0 \cdot s^{-1}$)	Q_{10}
Grey mullet	Red	2.9±0.2(11)	5.0±0.2(8)	1.7
	White	4.6±0.3(10)	8.4±0.5(5)	1.8
Blue Crevally	Red	2.0±0.2(6)	4.3±0.3(6)	2.2
	White	4.0±0.3(8)	7.6±0.4(5)	1.9
Dolphin fish	Red[a]	3.1±0.2(6)		
	White[a]	8.2±0.3(13)		
Skipjack tuna	Deep red	1.7±0.2(6)	4.9±0.4(11)	2.9
	White	3.3±0.2(10)	8.1±0.7(10)	2.5

[a] measured at 25 °C

Unloaded contraction velocity (V_{max}) for *N. neglecta* white fibres at 0–5 °C is similar to the warm water species measured at 10–20 °C (Fig. 5). Over the range 20–30 °C, V_{max} for white fibres from the tropical species were 2–3 times faster than those from the Antarctic fish measured at their normal body temperatures (≦2 °C) (Fig. 5).

The temperature dependence of V_{max} was similar for red and white muscle fibres of the Blue Crevally. Plots of $\log_{10} V_{max}$ vs $1/T$ were linear over the range 5–30 °C (Fig. 6). In contrast, V_{max} for the internal red muscle of Skipjack tuna had a higher $Q_{10(20-30 °C)}$ than for either white or superficial red fibres (Fig. 7). Q_{10} for V_{max} for equivalent fibre types were somewhat higher for Skipjack tuna and Kawakawa than for the other warm water species studied that do not maintain elevated muscle temperatures (Table 2).

Discussion

A number of studies have measured the contractile properties of myotomal strips (Wardle 1975; Brill and Dizon 1979). These are useful in determining myotomal contraction time which can be used together with a knowledge of stride length to predict maximum swimming speeds (Wardle 1975). However, the arrangement of muscle fibres within fish myotomes is complex. White fibres make varying angles (from 0 to >40°) with the longitudinal axis of the body (Alexander 1969). Strips of myotomal muscle therefore make unsuitable preparations for determining muscle mechanical properties since the orientation of fibres is undefined, the percentage of cut or damaged fibres high, and the centres of strips anoxic. In the present study, single fast fibres have been utilised which avoids these problems. Furthermore, the use of skinned preparations allows the properties of the contractile proteins to be studied in isolation from nerve and membrane effects.

Maximum Ca^{2+}-activated tension (P_0) of fish fast fibres are similar when measured at the normal body temperature of each species (Table 1) and within the range found for other twitch fibres from ectotherms (Hellam and Podolsky 1969). P_0 also shows only a moderate temperature dependence within the physiological range for at least the warm water species studied (Fig. 4).

Measured at 0–5 °C, unloaded contraction speeds (V_{max}) of *Notothenia* fast fibres are similar or higher than those of many temperate and tropical species at 10–20 °C (Fig. 5). However, an assessment of the degree of temperature compensation between species is complicated by their different life-styles and modes of locomotion. For example, *N. neglecta* is a relatively inactive benthic species whereas the tunas are fast swimming pelagic fishes. All available data on V_{max} of skinned muscle fibres at physiological body temperatures are shown in Fig. 8. Although within each temperature range, there is considerable variation in muscle V_{max}, the highest values are generally found for tropical species. Comparisons of V_{max} at low temperatures (<5 °C) indicates relatively modest compensations between Antarctic and tropical species (Fig. 5). However, values for P_0 at low temperature are generally much higher for Antarctic and cold-temperate fish (Fig. 4, Table 1 and Altringham and Johnston 1982). Thus it appears that the degree of temperature compensation for maximum power output (force × velocity) is more substantial.

It has recently been shown that for the desert iguana *Dipsosaurus dorsalis* muscle, V_{max} has a similar temperature dependence to that of burst running speed measured in the laboratory (Bennett 1980; Johnston and Gleeson 1984). However, fish with the highest V_{max} may not necessarily have the fastest burst locomotory speeds since any such correlation may be complicated by the segmental arrangement of the myomeres. For example, fibre geometry and myotome shape are likely to be important factors in determining the rate of deformation of each segment. It is noteworthy that at comparable temperatures, fast (white) muscle V_{max} for chain pickeral *Esox niger* is only 20–25% of that for most tropical species and yet the pickeral has a highly streamlined body shape and presumably a high maximum burst speed (Sidell and Johnston, submitted for publication).

It would appear that temperature related adjustments in V_{max}, P_0 and regulatory properties involve substantial changes in protein chemistry.

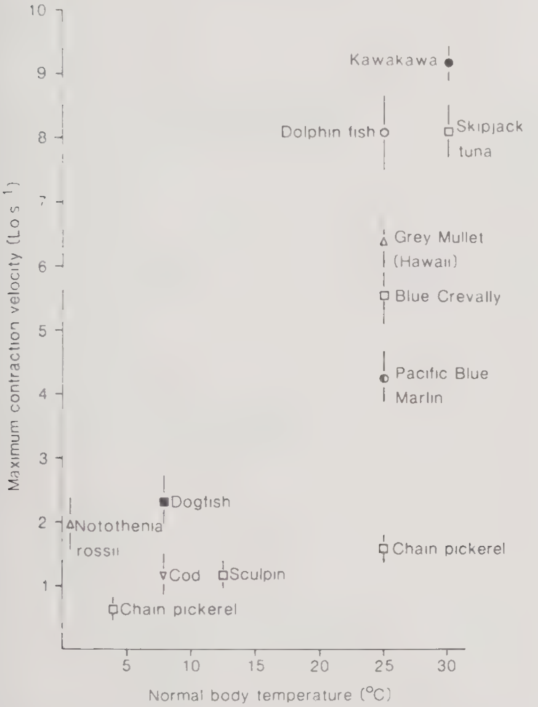

Fig. 8. Comparison of unloaded contraction speeds of various fish white muscle measured at their normal body temperatures. Data not from the present study was from the following sources: Chain pickeral (*Esox niger*, freshwater lakes, Maine, USA 4–30 °C) (Sidell and Johnston, to be published); Dogfish (*Scyliorhinus canicula*, North Sea, 2–15 °C) (Altringham and Johnston 1982); Cod (*Gadus morhua*, North Sea, 2–15 °C) (Altringham and Johnston 1982); Sculpin (*Myoxocephalus scorpius*, North Sea, 2–15 °C) (Johnston and Sidell 1984); Pacific Blue Marlin (*Maikaira nigrans*, Pacific Ocean) (Johnston and Salamonski, unpublished results)

For example, the temperature at which the Ca^{2+}-regulation of contraction becomes disrupted varies from 15 °C for Antarctic to 25 °C for cold-temperate species, whilst warm water fish and the desert iguana show full Ca^{2+}-control up to 30 and 45 °C, respectively (Fig. 3; Johnston and Sidell 1984; Johnston and Gleeson 1984). The half-life of thermal inactivation of myofibrillar ATPase activity under comparable conditions varies from around 1–2 min for Antarctic fish to several hours for tropical species (Johnston and Walesby 1977).

V_{max} of tuna fast muscles is not particularly different from that of other tropical species that do not maintain elevated muscle temperatures (Figs. 7 and 8). Similar results have been obtained for burst swimming speeds. For example, Walters and Fiersteine (1964) measured maximum speeds of 21 bodylengths$\cdot s^{-1}$ for yellowfin tuna and 19 bodylengths$\cdot s^{-1}$ for Wahoo (*Acanthocybium solandri*). The Wahoo lacks the specialised circulatory system necessary to maintain warm muscles (Collette 1978). Therefore, at first glance, it would appear that the advantage of warm muscles is not so much with increased power development per se. However, the effects of elevated muscle temperatures on high speed swimming abilities may be more complex. Only 5–7% of the total muscle is composed of red fibres in Wahoo (unpublished observations) compared to 25–33% for tuna. In most fish, the red fibres will be contracting passively when the fish is swimming at burst speeds. This would be a disadvantage for species such as tuna in which a high proportion of the tissue is red muscle. However, it appears that the high Q_{10} for V_{max} and the temperature gradient between internal red muscle and white muscle may allow both fibre types to contract at similar speeds. Therefore, both white and internal red muscle fibres may contribute to power generation at high speeds. Data on the temperature gradient between internal red and white muscle in free swimming fish at different water temperatures and activity levels would be needed to test this hypothesis. However, other advantages have been suggested for the evolution of warm muscles which include a faster catabolism of lactic acid and enhanced myoglobin mediated oxygen flux from capillary to mitochondrion (Stevens and Carey 1981).

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8445

Stomiatoidea: Development

K. KAWAGUCHI AND H. G. MOSER

FISHES of this group of midwater predators are characterized by their dark coloration, serial photophores, large jaws, fang-like teeth, and chin barbels. Traditionally they have been grouped in six families allied to the lightfishes and hatchetfishes (Weitzman, 1974), and together are now considered monophyletic and given ordinal status (Rosen, 1973; Fink and Weitzman, 1982). Fink (this volume) gives evidence for reducing the six stomiatoid families to one. Because knowledge of stomiatoid ontogeny lags far behind that of the adults, for convenience of discussion we use Weitzman's (1974) grouping of the families

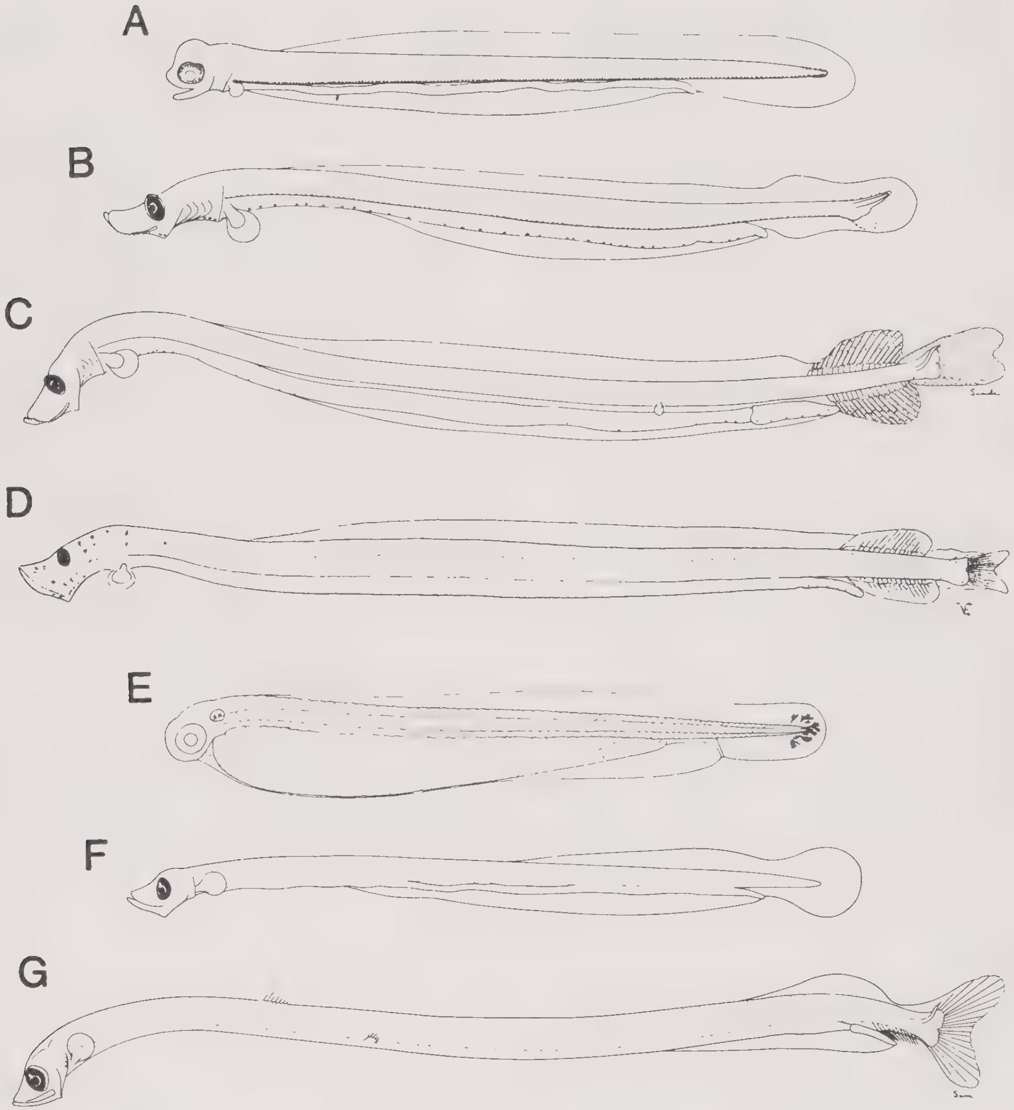

Fig. 89. Larvae of *Stomias* and *Chauliodus*. (A) *S. atriventer*, 4.6 mm, CalCOFI 7501 Sta. 97.60; (B) *S. atriventer*, 10.0 mm, CalCOFI 6604 Sta. 107.65; (C) *S. atriventer*, 22.2 mm; CalCOFI 6604 Sta. 107.65; (D) *S. ferox*, 30 mm, from Ege, (1918); (E) *C. sloani*, 6.0 mm; from Mito (1961a); (F) *C. macouni*, 15.0 mm, CalCOFI 6204 Sta. 60.60; (G) *C. macouni*, 45.2 mm, CalCOFI 5707 Sta. 67.60.

Astronesthidae, Stomiatidae, Chauliodontidae, Melanostomiatidae, Malacosteidae, and Idiacanthidae, in the Superfamily Stomiatoidea.

EGGS

Eggs are known for *Chauliodus*, *Stomias*, and *Tactostoma* and have in common a round shape, smooth chorion, and segmented yolk, *Chauliodus* eggs have a wide perivitelline space and lack an oil globule. Egg diameters are: *C. sloani*, 2.2–2.5 mm (Sanzo, 1931d); *C. barbatus*, 3.1–3.6 mm (Pertseva-Ostroumova and Rass, 1973); *C. macouni*, 2.7–3.1 mm, with an initial yolk diameter of 1.3–1.5 mm (original data). Mito (1961a) described an egg, referred to *C. sloani*, 2.12 mm in diameter with no oil globule but with a second membrane. *Stomias* eggs have a second membrane, a single oil globule and the following diameters: *S. colubrinus*, 1.3–1.5 mm, with inner membrane 1.05–1.1 mm (Pertseva-Ostroumova and Rass, 1973); *S. atriventer*, 0.88–0.92 mm, inner membrane diameter is 0.82–0.84

TABLE 44. MERISTIC COUNTS OF STOMIATOID GENERA. Most frequent count or range is followed by overall range or infrequent count in parentheses. Data from Gibbs (1964a,b), Gibbs et al. (1983), Morrow (1964a, b, c), Morrow and Gibbs (1964), Bolin (1939a), Imai (1941), original counts.

Family and genus	Vertebrae	Fin rays			
		Dorsal	Anal	Pectoral	Pelvic
Stomiatidae					
Macrostomias	164	13,14	16 (15–18)	7 (6)	4
Stomias	64–83	17–20 (16–22)	19–21 (18–25)	6–7 (6–9)	5 (4)
Chauliodontidae					
Chauliodus	51–62	6,7 (5–7)	10–12 (10–13)	12,13 (11–14)	7 (6–8)
Astronesthidae					
Astronesthes	46–58	15 (10–21)	12–22	8 (5–9)	7 (6–8)
Borostomias	53–55	13 (10–14)	13–16 (10–19)	7 (6–9)	7
Heterophotus	66	11 (13)	12–15 (17)	7	7
Neonesthes	53	9–11 (12)	25–27 (22–28)	8 (7)	7 (6–8)
Rhadinesthes	67	11 (12,13)	18 (19–21)	7 (6–8)	7
Melanostomiatidae					
Bathophilus	38–45 (33–50)	13–16 (9–18)	15–16 (9–18)	1–37	11–16 (4–26)
Chirostomias	54–55	18–20	22–26	6	7
Echiostoma	57–59	11–14 (11–16)	13–18 (13–19)	I+3	8
Eustomias	56–69	21–25 (20–30)	32–46	0–13	7 (6–8)
Flagellostomias	65	16 (14–17)	23–25 (21–26)	I+8–9+II	7
Grammatostomias	50–56	18–21	21–23 (20–24)	4–11	7–8
Leptostomias	77–80 (75–83)	16–22	20–29	10 (9–11)	7 (8)
Melanostomias	50–57	12–17	16–20	5 (4–6)	7 (8)
Opostomias	60	21	24	I+4	8
Pachystomias	48	22 (21–24)	27 (25–29)	5–6	8–9 (7)
Photonectes	49–64	15–24	17–24	0–3	7 (6)
Tactostoma	80–82	14–16	19–22	0	8–10
Thysanactis	61	17–18	21–25	I+10,11	7
Trigonolampa	61–62	19–20 (18)	18 (19)	5	7
Malacosteidae					
Aristostomias	44–56	18–26	24–32	6–10 (3–17)	6
Malacosteus	49	14–19 (20)	17–21 (23)	3–4 (5)	6
Photostomias	52–58	22–28	25–32	0	6
Idiacanthidae					
Idiacanthus	79–85	54–74	34 (33–39)	0	6

mm, oil globule diameter of 0.20–0.25 mm, initial yolk diameter of 0.70 mm (original data). *Tactostoma macropus* eggs have a single membrane, 1.44–1.54 mm in diameter, an oil globule 0.30–0.40 mm in diameter and an initial yolk diameter of 0.78–0.80 mm (original data). Eggs of *C. macouni* and *S. atriventer* are illustrated in Matarese and Sandknop (this volume).

LARVAE

Larvae of Stomiatoidea occur in the upper water column, some at the surface. In most groups the larvae are elongate, have a large head, elliptical eyes that protrude slightly from the dorsal head profile, an elongate, straight gut (trailing from the body in some species), a well developed finfold, large paddle-shaped pectoral fins that lack rays until transformation, and late-forming pelvic fins. Melanophore patterns provide a useful set of characters and genera usually have a distinct pattern. The larval melanophores are retained in a subcutaneous position in transforming specimens and provide a means for identifying larvae. During transformation, photophores form simultaneously and initially are unpigmented. Counts of fin rays, vertebrae, and photophores are summarized in Tables 44 and 45.

Stomiatidae (Fig. 89).—Larvae of five species are known (Table 46). Larvae are 3–4 mm at hatching and have an elongate yolk sac. The slender body is round in cross-section, but becomes slightly deeper by late postflexion. The head is relatively small with a slightly flattened snout. The eyes are elliptical. The elongate gut extends almost the entire length of the body and has a slightly enlarged terminal section that reaches the anal fin origin. The median finfold is small and best developed posteriorly. The opposing dorsal and anal fins develop far posteriad on the body in early postflexion larvae, but the pelvic fins do not appear until just before transformation.

Late-stage embryos of *Stomias* have melanophores along the dorsum, which migrate ventrad and form a distinct series between the body and gut. This series extends to the tip of the notochord. The series is lost before notochord flexion but, in most species, another sparser series develops along the ventral midline of the gut, from the isthmus to the anus. *S. boa* and *S. ferox* develop a mid-lateral series of melanophores along the body and *S. colubrinus* has scattered melanophores along the entire hypaxial body region. These species also develop extensive dorsal and lateral head pigment. All species form scattered pigment on the dorsal, anal, and caudal fins.

A 75-mm specimen (MCZ Cat. No. 59858) with an extremely slender body form (body depth 1.3% of body length) has fin and

TABLE 45. PHOTOPHORE COUNTS OF STOMIATOID GENERA. Most frequent count or range is followed by overall range or infrequent count in parentheses. Data sources as in Table 1. Photophore groups as defined by Morrow (1964a).

Family and genus	Photophore groups					
	IP	PV	VAV	AC	OV	VAL
Stomiatidae						
Macrostomias	11 (12)	80–86	58–67	19–22	79–85	58–68
Stomias	9–13	32–51	5–16	14–20	32–50	4–17
Chauliodontidae						
Chauliodus	8–11	17–23	22–30	8–13	17–21	22–29
Astronesthidae						
Astronesthes	5–12	6–20	7–27	7–13	5–19	7–26
Borostomias	10–13	20–31	15–25	9–15	21–29	16–25
Heterophotus	10–11	32–35	13–14	12–15	33–36	16–20
Neonesthes	9–12	14–17	16–21	13–18	13–15	13–21
Rhadinesthes	10 (6)	25 (26)	20–23	16	22–24	27
Melanostomiatidae						
Bathophilus	5 (4–6)	12–18	11–13 (11–17)	5–7 (5–9)	13–14 (10–16)	9–11 (8–17)
Chirostomias	9 (8)	25–27 (28)	19–20 (16)	9 (10)	23 (24–25)	19–20 (16)
Echiostoma	8+2	25–28	14–18	12–13 (11)	24–31	13–17 (18)
Eustomias	7–8 (9)	27–33 (24–36)	13–17 (11–21)	17–23 (15–25)	26–33 (24–37)	13–18 (12–22)
Flagellostomias	9–10 (8)	31–34	14–16	16–18 (15)	31–32 (30)	14–15 (12–17)
Grammatostomias	7 (6)	15–18	19–22	10–13	15–18	19–22
Leptostomias	10 (11)	42–45 (39–48)	20–23 (24)	11–13 (14)	40–43 (39–48)	20–22 (23–24)
Melanostomias	8+2 or 3	23–30	12–15	9–11	22–28	11–15
Opostomias	4+4	27	17	16	27	17
Pachystomias	8–9	14–16 (17)	13–14	8–9	17–18	14–15
Photonectes	8–11	19–24, 34–38	11–15 (16–18)	10–13 (9)	19–24 (17), 30–36	11–14 (15–17)
Tactostoma	8	46	19	12	43	18
Thysanactis	20	31–32	14–16	11–12	30–32	14–16
Trigonolampa	11	23–24 (22)	22 (24)	10–11	22–24	23–24 (26)
Malacosteidae						
Aristostomias	5+3	15–17 (14–19)	15–18	9–11 (12)	16–19 (14–20)	15–17 (14–18)
Malacosteus	(Serial photophores absent or uncountable)					
Photostomias	5+2	13–16	21–25	12–15	12–17	20–23
Idiacanthidae						
Idiacanthus	IP+PV = 31–36		16–18 (15)	13–18	22–25	31–35 (30–36)

vertebral counts that match *Macrostomias longibarbatus*. Its morphology is that of a highly attenuate *Stomias* larva. Pigmentation is restricted to a series of small melanophores along the ventral midline of the gut. The ventral photophore rows are beginning to form.

Chauliodontidae (Fig. 89).—Larvae of five species are known (Table 46). Larvae are 6–7 mm long at hatching, with an elongate yolk sac. The body is slender with a circular cross-section, and remains so throughout development. The head is relatively small, with elliptical eyes and a short, acute snout. The gut has a smaller diameter than in *Stomias* but is relatively longer. The short terminal section extends beyond the anal fin origin. The median finfold is small and best developed rearward on the body. The dorsal, anal, and pelvic fins form in late postflexion larvae in the adult position. A fan-shaped array of melanophores occurs in the caudal region of yolk-sac larvae but is soon lost. No other pigment develops. Larvae of some species reach 46 mm SL and there appears to be marked shrinkage at transformation.

Astronesthidae (Fig. 90).—Astronesthid larvae have been illustrated and described briefly by Roule and Angel (1930), Whitley (1941), Pertseva-Ostroumova and Rass (1973), and Belyanina (1982b); however only two of these were identified to genus (Table 46). We have examined more than 10 types of astronesthid larvae, 7 of which are listed in Table 46. Astronesthid larvae display a great variety of structure and pigmentation, but hold in common the advanced position of the dorsal fin, in contrast to other Stomiatoidea, except *Chauliodus*. The types differ fundamentally in gut shape and body form: Types I and II are laterally compressed, relatively deep-bodied, and have a non-trailing or slightly trailing gut with terminal section as in melanostomiatids; Types III–VII have a slender body and a trailing gut; in Types III–V the gut is deflected ventrad from the body just anterior to the anal fin base and in Type VI and VII at midbody, anterior to the dorsal fin (Figure 90).

Type I (Fig. 90A).—larvae up to 26.5 mm; laterally compressed; head shallow with acute snout; eyes relatively large, slightly

→

Fig. 90. Larvae of Astronesthidae. (A) Type I, 23.7 mm, ORI A105; (B) Type II, SIO Tasaday I A3; (C) Type IV, 33.0 mm, MCZ Cat. No 59855; (D) Type V, 22.0 mm, Dana Sta. 3931; (E) Type VII, 28 mm, MCZ Cat. No. 59856.

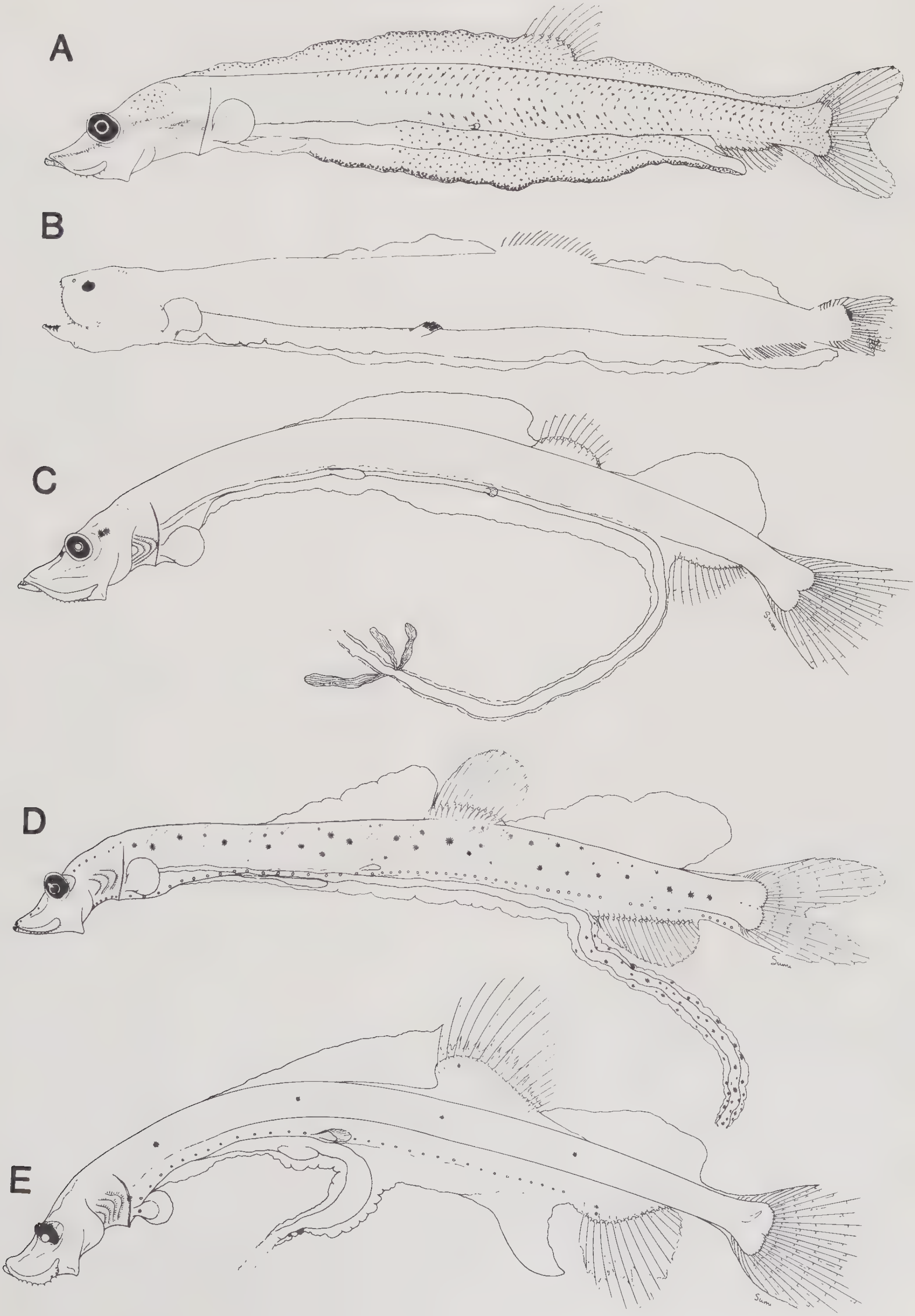
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Table 46. Pigment Characters and Gut Structure in Larvae and Transforming Specimens of Stomiatoidea. (NT = not trailing, ST = slightly trailing, T = trailing freely).

Species	Length of larvae (mm)	Length of transforming specimens (mm)	Dorsal myomere melanophores (no./myomere)	Epaxial myoseptum melanophores (no./myoseptum)	Hypaxial myoseptum melanophores (no./myoseptum)	Gut structure	Source
Stomiatidae							
Stomias boa	—	38	0	0	0	NT	Sanzo, 1912a
Stomias boa	10.4–30.4	41.5	0	0	0	NT	Sanzo, 1931d
Stomias boa	9.0–32	—	0	0	0	NT	Ege, 1918
Stomias ferox	9.0–44	—	0	0	0	NT	Ege, 1918
Stomias colubrinus	3.3–16	—	0	0	0	NT	Pertseva-Ostroumova and Rass, 1973
Stomias atriventer	4.6–32	—	0	0	0	NT	original
Macrostomias longibarbatus	—	75	0	0	0	NT	original
Chauliodontidae							
Chauliodus sloani	33.6	41.6	0	0	0	NT	Sanzo, 1915a
Chauliodus sloani	5.7–41.6	27.1	0	0	0	NT	Sanzo, 1931d
Chauliodus sloani	2.1	—	0	0	0	NT	Mito, 1961a
Chauliodus danae	22.5–25	—	0	0	0	NT	Belyanina, 1977
Chauliodus macouni	38.0–49	35–44	0	0	0	NT	Belyanina, 1977
Chauliodus minimus	23.5–35	—	0	0	0	NT	Belyanina, 1977
Chauliodus pammelas	10.6–40	—	0	0	0	NT	Belyanina, 1977
Chauliodus sloani	7.4–35	27–34.2	0	0	0	NT	Belyanina, 1977
Chauliodus macouni	5.6–46	—	0	0	0	NT	original
Astronesthidae							
Unidentified	14.0–23	—	0	0	0	T, NT	Roule and Angel, 1930
Astronesthes lupina	20	—	0	0	0	T	Whitley, 1941
Borostomias panamense	5.0–17	—	0	0	0	T	Pertseva-Ostroumova and Rass, 1973
Unidentified	16	—	?	+	+	NT	Belyanina, 1982b
Unidentified	17.7	—	2 total	0	0	T	Belyanina, 1982b
Type I	12.3–26.5	—	several	several to many	several to many	NT	original
Type II	14.9–26	29, 40	0	0	0	ST	original
Type III	16.2	20.5, 22.5	0	0	0	T	original
Type IV	14.4–34.5	40.5	0	0	0	T	original
Type V	17.4–19.4	20, 22	0	0	0	T	original
Type VI	—	28	0	0	0	T	original
Type VII	—	28	0	0	0	T	original
Melanostomiatidae							
Tactostoma macropus	5.0–44	49	0–1	0	1–3	NT	original
Melanostomias spilorhynchus	17	21–32	1	0	ca. 3	NT	Beebe and Crane, 1939
Melanostomias biseriatus	—	21–25	1	0	ca. 3	NT	Beebe and Crane, 1939
Melanostomias valdiviae	—	25	1	0	2–3	NT	original
Melanostomias sp.	13.4–17.2	16.4–22	1	0	2–4	NT	original
Echiostoma tanneri	20, 25	—	1	0	2–5	NT	Beebe and Crane, 1939
Echiostoma sp.?	13.8	—	1	0	2–4	NT	Belyanina, 1982b
Echiostoma barbatum	—	34	1	0	1–2	NT	original
Photonectes dinema	—	24 and >	1 (?)	0	3–4	NT	Beebe and Crane, 1939
Photonectes leucospilus	—	25 and >	1 (?)	0	3–4	NT	Beebe and Crane, 1939
Photonectes albipinnis	—	16–22	1	0	2–3	NT	original
Photonectes sp.	11.0–12.5	—	1	0	4–5	NT	original
Photonectes parvimanus	12.0–26	25	3–6	0	3–4	NT	Beebe and Crane, 1939
Photonectes parvimanus	27	—	3–4	0	2–4	NT	original
Photonectes parvimanus	—	28	1–2	0	2–4	NT	original
Photonectes sp.	5.4–22.2	—	ca. 7	0	5–7	NT	original
Opostomias mitsuii	15.0–21	—	1	0–1 (2–3 posteriorly)	1–2 (3–5 post.)	NT	original
Flagellostomias boureei	20.0–21	34, 39	1	0	1	NT	Beebe and Crane, 1939
Flagellostomias boureei	10.8–36.4	—	1	0	1–2	NT	original
Odontostomias micropogon	—	42	1	1–?	2–4	NT	Beebe and Crane, 1939
Leptostomias gladiator	12.0–30	38–45	1+several	1–5	2–4	NT	Beebe and Crane, 1939
Leptostomias gracilis	—	37.8	1+1–5	5–7	6–9	NT	original
Leptostomias sp.	25	—	1+1–3	4–5	4–6	NT	original
Bathophilus nigerrimus	11.6	21.7	1 or >	0	0	NT	Sanzo, 1915a
Bathophilus nigerrimus	5.9, 14.0	19.2–21.7	1 or >	0	0	NT	Sanzo, 1931d

TABLE 46. CONTINUED.

Species	Length of larvae (mm)	Length of transforming specimens (mm)	Dorsal myomere melanophores (no./myomere)	Epaxial myoseptum melanophores (no./myoseptum)	Hypaxial myoseptum melanophores (no./myoseptum)	Gut structure	Source
Bathophilus metallicus	—	25	3 or >	0	0	NT	Beebe and Crane, 1939
Bathophilus sp.	11, 12	—	1 or >	0	0	NT	Beebe and Crane, 1939
Bathophilus sp.	7	—	1 or >	0	0	NT	Beebe and Crane, 1939
Bathophilus sp.	15	—	(?)	0	0	NT	Roule and Angel, 1930
Bathophilus sp.	18.2	—	1 or >	0	0	NT	de Sylva and Scotten, 1972
Bathophilus filifer	4–10	—	1 or >	0	0	NT	Pertseva-Ostroumova and Rass 1973
Bathophilus brevis	15.7	—	1 or >	0	0	NT	original
Bathophilus flemingi	2.9–23.8	—	1 to several	0	0	NT	original
Eustomias sp.	33	—	7 total	0	0	T	Regan, 1916
Eustomias sp.	13	—	7 total	0	0	T	Beebe and Crane, 1939
Eustomias spp. (4 types)	6.0–45	—	5–11 total	0	0	T	original
Malacosteidae							
Aristostomias scintillans	4.3–47	45	14 total to many	0	0	T	original
Photostomias guernei	20.0–27.5	30, 31	8 pairs total	0	0	T	original
Unidentified	12	—	12 total	0	0	T	Beebe and Crane, 1939
Unidentified	34.5	—	0	0	0	T	original
Idiacanthidae							
Idiacanthus fasciola	16.0–28	35–48	0	0	1	T	Beebe, 1934
Idiacanthus sp.	7.0–39	—	0	0	1	T	Pertseva-Ostroumova and Rass, 1973
Idiacanthus antrostomus	4.5–71	67–>	0	0	1	T	original

elliptical; gut moderately slender, thin-walled; finfold moderate; pigment pattern consists entirely of minute melanophores, increasing in number with development, principally in the expaxial and hypaxial myosepta; other pigment above brain, paired internal streaks in snout, melanophores in dorsal and ventral finfold, dorsal fin base, and on posterior half of gut.

Type II (Fig. 90B).—larvae reach at least 26 mm; deep-bodied and laterally compressed in late-stage larvae; head deep; eyes small, slightly elliptical; gut slightly trailing and with larger diameter than in Type I; dorsal finfold relatively deep; pigment above brain, along lower jaw and at angular and gular region; blotch at posterior margin of superior hypural complex and one midway out on inferior group of caudal rays; fin ray and vertebral counts and photophore counts match *Astronesthes gemmifer.*

Type III.—larvae reach at least 16.2 mm; body slender; head and eyes moderate in size; eyes elliptical; slender gut trails free from body at anal fin origin; finfold moderately developed, except posterior to dorsal fin the finfold appears as an enlarged adipose fin; pigment restricted to a series of melanophores along lower jaw and between upper and lower hypural complexes; counts match *Astronesthes richardsoni.*

Type IV (Fig. 90C).—larvae reach 40 mm; morphology similar to Type III, except head relatively longer and eyes almost round; gut with leaf-like appendages on trailing section; pigment restricted to postorbital blotch and interorbital band; fin and vertebral counts and photophore arrangement match *Heterophotus.*

Type V (Fig. 90D).—larvae reach about 20 mm; morphology as in Types III and IV; eyes slightly elliptical; pigment heavy; melanophores on head, lateral to posterior brain region, on snout and lower jaw symphysis; lateral surface of body covered with an irregular pattern of large melanophores; melanophores on trailing gut. Pertseva-Ostroumova and Rass (1973) identified larvae of this type as *Borostomias panamense.*

Type VI.—specimen transforming at 28 mm; morphology similar to Types II–V, except trailing gut deflected from body far in advance of anal fin origin; eyes elliptical; dorsal finfold highly developed and ventral finfold anterior to anal fin is rudder-like; pigment lacking; meristics indicate it is in the genus *Astronesthes.*

Type VII (Fig. 90E).—specimen transforming at 28 mm; morphology similar to Type VI; dorsal and anal fins supported on cartilaginous pedestals; a series of 4 melanophores along horizontal septum; some melanophores on anterior region of dorsal and anal fin bases and on preanal finfold. Whitley (1941) described a larva similar to this as *Astronesthes lupina.*

Melanostomiatidae (Figs. 91–92).—Larvae have been identified for 10 of the 15 genera (Table 46). *Bathophilus* was the first to be identified (Sanzo, 1915a). The only comprehensive work on melanostomiatid ontogeny is that of Beebe and Crane (1939) who identified larvae of 8 genera and 5 species by the use of transforming series. Since then, the only other melanostomiatid larvae that have been described are *Bathophilus filifer* (Pertseva-Ostroumova and Rass, 1973), *Bathophilus* sp. (de Sylva and Scotten, 1972), and *Echiostoma* (?) sp. (Belyanina, 1982b). Descriptions of *Opostomias* and *Tactostoma* are included in this paper. Larvae of *Tactostoma* were initially identified by E. H. Ahlstrom.

Larval representatives of the 10 genera are highly various in form and pigmentation, however, with the exception of *Eustomias,* they share the following structural features: body elliptical in cross-section; head laterally compressed; eyes small and elliptical; gut terminated in an elongate muscular bulb that may extend beyond the anal fin origin but not beyond the margin of the finfold; dorsal and anal fins form in adult position posteriorly on the body; body pigment consists of one or more melanophores dorsal to each myomere, one or more melanophores on the hypaxial myosepta and, in some genera, on the epaxial myosepta. Dorsal and lateral pigmentation tends to be heavier in forms with higher meristic counts. The genera differ principally in body size, relative body depth, relative head size, jaw size, gut diameter, size and shape of the terminal gut section, finfold height, and pigment pattern.

Present knowledge indicates that genera apparently have distinct facies, tentative descriptions of which are presented below. Confirmation awaits identification of additional species.

Tactostoma (Fig. 91A).—larvae reach 44 mm in length; body extremely slender; head flat and elongate initially, becoming less flat and relatively smaller with development; eye size moderate; gut slender; finfold moderate; pectoral fin lost at transformation; early larvae develop one melanophore per myomere along dorsum and 1–3 melanophores on the hypaxial myosepta; postflexion larvae gradually lose the dorsal melanophores and then the hypaxial myosepta pigment, in contrast with other genera in which body pigment increases with development; pigment on lower jaw symphysis, isthmus, pectoral fin base, cleithrum, and above gut terminus; dorsal and ventral pigment accentuated at caudal peduncle.

Melanostomias (Fig. 91B).—transforming specimens as small as 16.4 mm; body slender; head small; snout short; eye size moderate; gut slender; finfold relatively small; one melanophore per myomere along dorsum in one form and in another form the zone between the 7th–10th myomere and the dorsal fin lacks dorsal pigment; 2–3 melanophores in hypaxial myosepta; pigment above and below head, below liver, on terminal gut section, and along finfold margins. Larvae tentatively identified as *Echiostoma* have similar characters (Table 46).

Photonectes (Fig. 91C).—larvae of different forms transform at sizes between 16 and 28 mm; body somewhat deep; head size and snout length moderate; eyes small, highly elliptical; several forms of dorsal myomere pigment (1 melanophore per myomere in Subgenus *Photonectes* and 3–7 per myomere in Subgenus *Trachinostomias*); hypaxial myosepta with 2–7 melanophores depending on form (Table 46); extensive pattern of minute melanophores on head, finfold, and median fins.

Flagellostomias (Fig. 91D).—larvae may reach 30–40 mm; body somewhat deep; head large, deep, with steeply sloping snout and large jaws; eyes small; gut diameter relatively large; finfolds large, accentuating body depth; one large melanophore per myomere along dorsum; 1–3 melanophores in hypaxial myosepta; some scattered lateral melanophores in median fin region; other pigment scant; a few melanophores in head region, some on finfold in posterior gut region, and on dorsal and anal fins.

Opostomias (Fig. 91E).—body moderately deep; head large, deep posteriorly with elongate sloping snout; eyes small; gut slender; finfold large; one melanophore per myomere along dorsum; 1–2 melanophores in hypaxial myosepta; epaxial and hypaxial myosepta below dorsal fin base have several melanophores, giving this region a banded appearance; melanophores on dorsal head region, gill arch and gut terminus.

Leptostomias (Fig. 91F).—larvae may reach about 40 mm; body somewhat deep; head moderately large, deep; eyes small; gut slender; finfold moderate; pigmentation heavy; one large melanophore and 1–5 smaller ones per myomere along dorsum; numerous melanophores on epaxial and hypaxial myosepta, increasing with development to completely outline myosepta; pigment extensive on dorsal and ventral head regions, on gill arches; pigment below liver, on finfold margins, above gut terminus and on dorsal and anal fins.

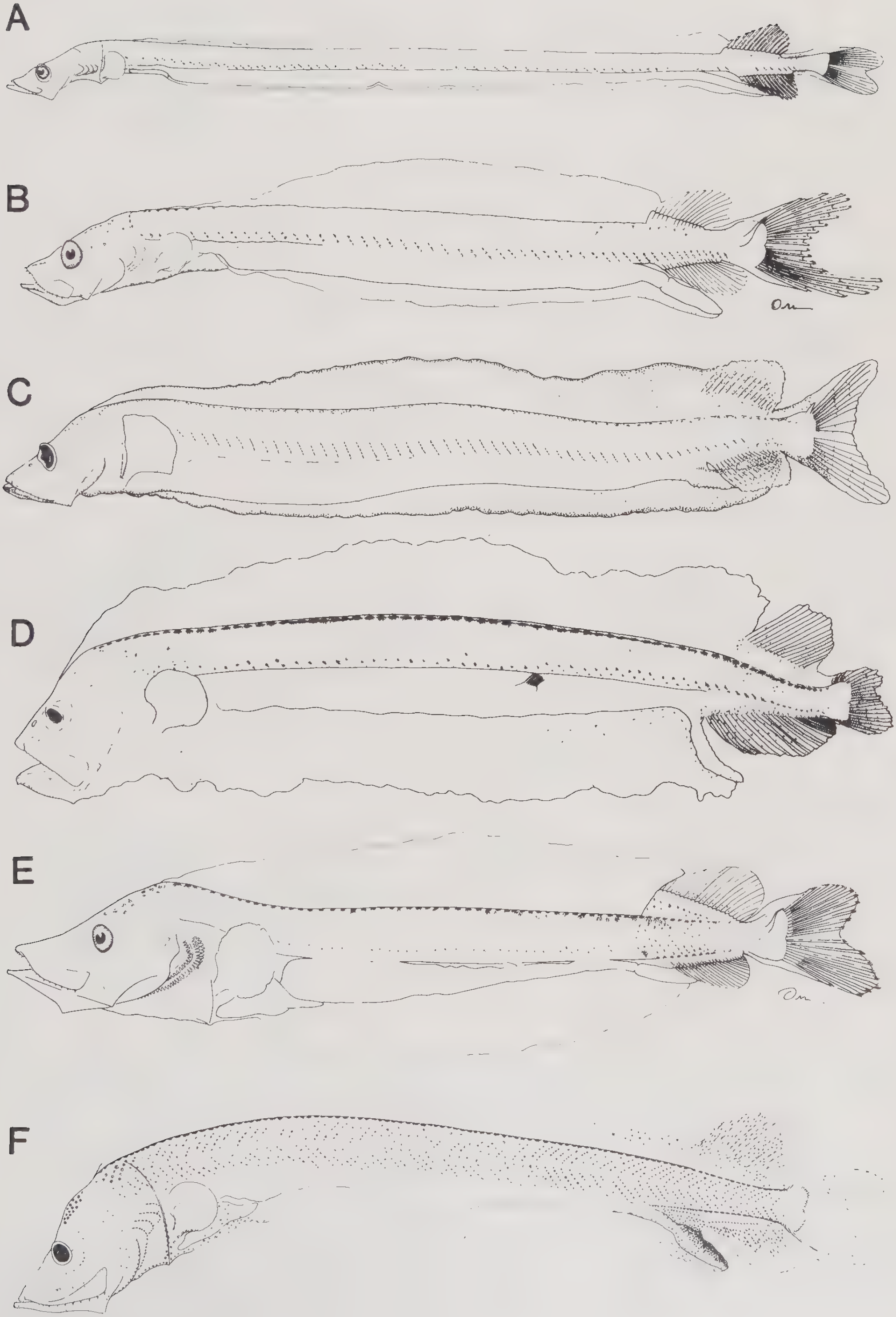
Bathophilus (Figs. 92A–C).—larvae transform at 25 mm or less; deep-bodied compared with other genera; head and jaws large; barbel forms in late postflexion larvae, particularly in *B. brevis*; eye size moderate; gut large to voluminous, with highly developed s-shaped terminal section; finfolds, particularly dorsal, large; one or several melanophores per myomere along dorsum and an opposing series of melanophores along ventral surface of myomeres; no lateral pigment; head, finfolds and median fins pigmented.

Eustomias (Fig. 92D).—larvae of some species reach 45 mm; body slender, and round in cross-section; head elongate and flat with large spatulate snout; large jaws; eyes moderate in size, slightly elliptical to round; gut slender, deflected ventrad at anal fin origin and trailing from body; body pigment consists of 5–11 large melanophores along the dorsal midline; usually pigment at lower jaw symphysis.

Malacosteidae (Fig. 93).—Larvae of this group have not been described, although the 12-mm larva illustrated by Beebe and Crane (1939) and referred to "?*Eustomias*" is apparently *Aristostomias.* We have examined larval series and transforming specimens of *A. scintillans* and *Photostomias guernei* (Table 46).

Aristostomias scintillans (Fig. 93A).—larvae reach 47 mm length; body slender; head large, flat; snout elongate; jaws large; eyes slightly elliptical; opercle markedly reduced; gut slender, deflected ventrad at anal fin origin and trailing from body; finfold moderate; dorsal and anal fins form in adult position at about flexion stage; pelvics form late; initial pigment pattern is a series of paired melanophores along the dorsum, beginning with 14

Fig. 91. Larvae of Melanostomiatidae. (A) *Tactostoma macropus,* CalCOFI Norpac Sta. 14; (B) *Melanostomias* sp., 16.0 mm, ORI KH73-2, Sta. 49-7; (C) *Photonectes* sp., 22.2 mm, SWFC, Albacore Oceanography Cruise 71, Sta. 99; (D) *Flagellostomias boureii,* 36.4 mm, SIO Cat. No. 73-329, Tasaday I, Tow 42; (E) *Opostomias mitsuii,* 15.0 mm, ORI KH 73-2 Sta. 2–3; (F) *Leptostomias* sp., 24.5 mm, MCZ Cat No. 59857.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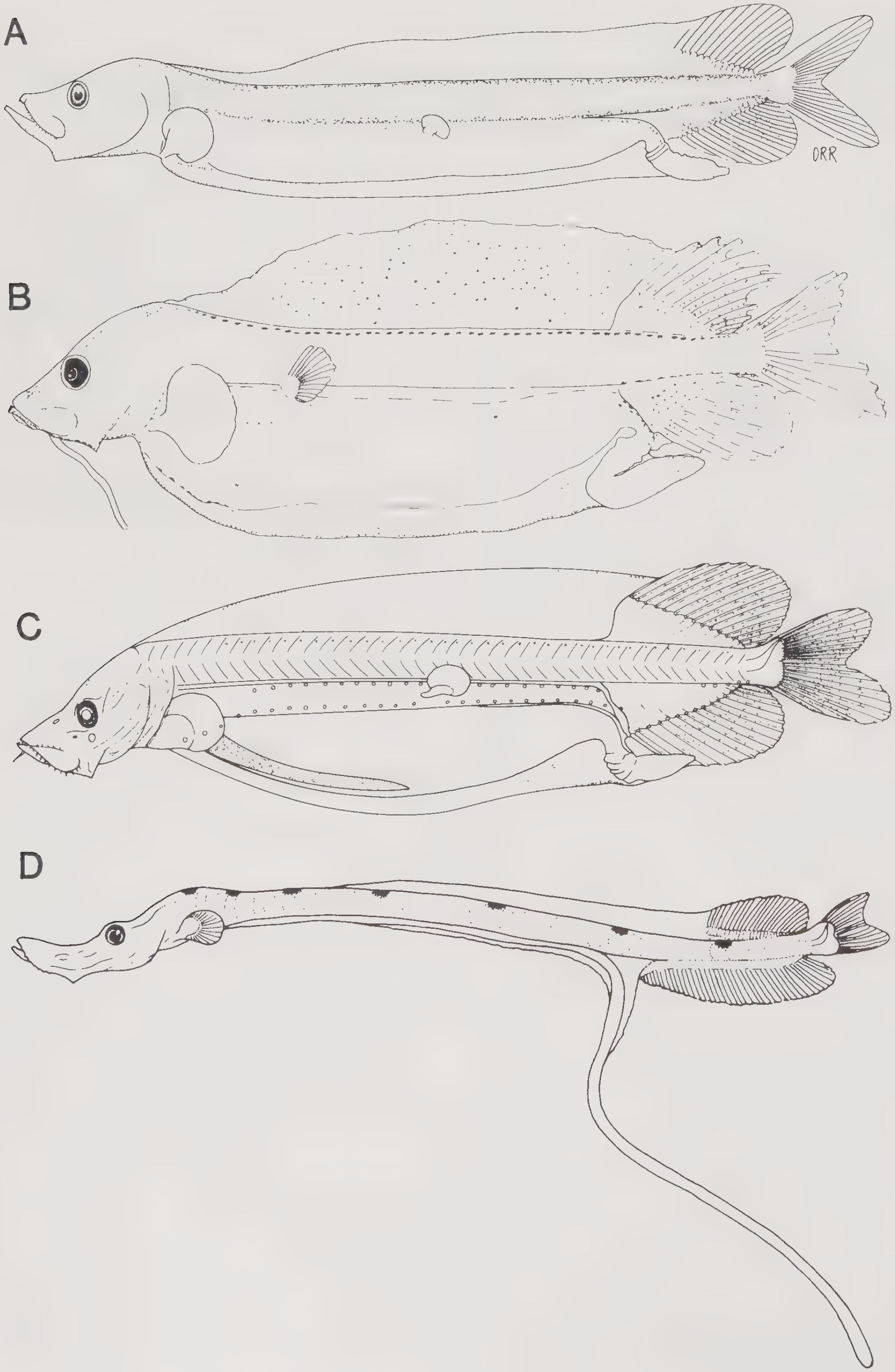
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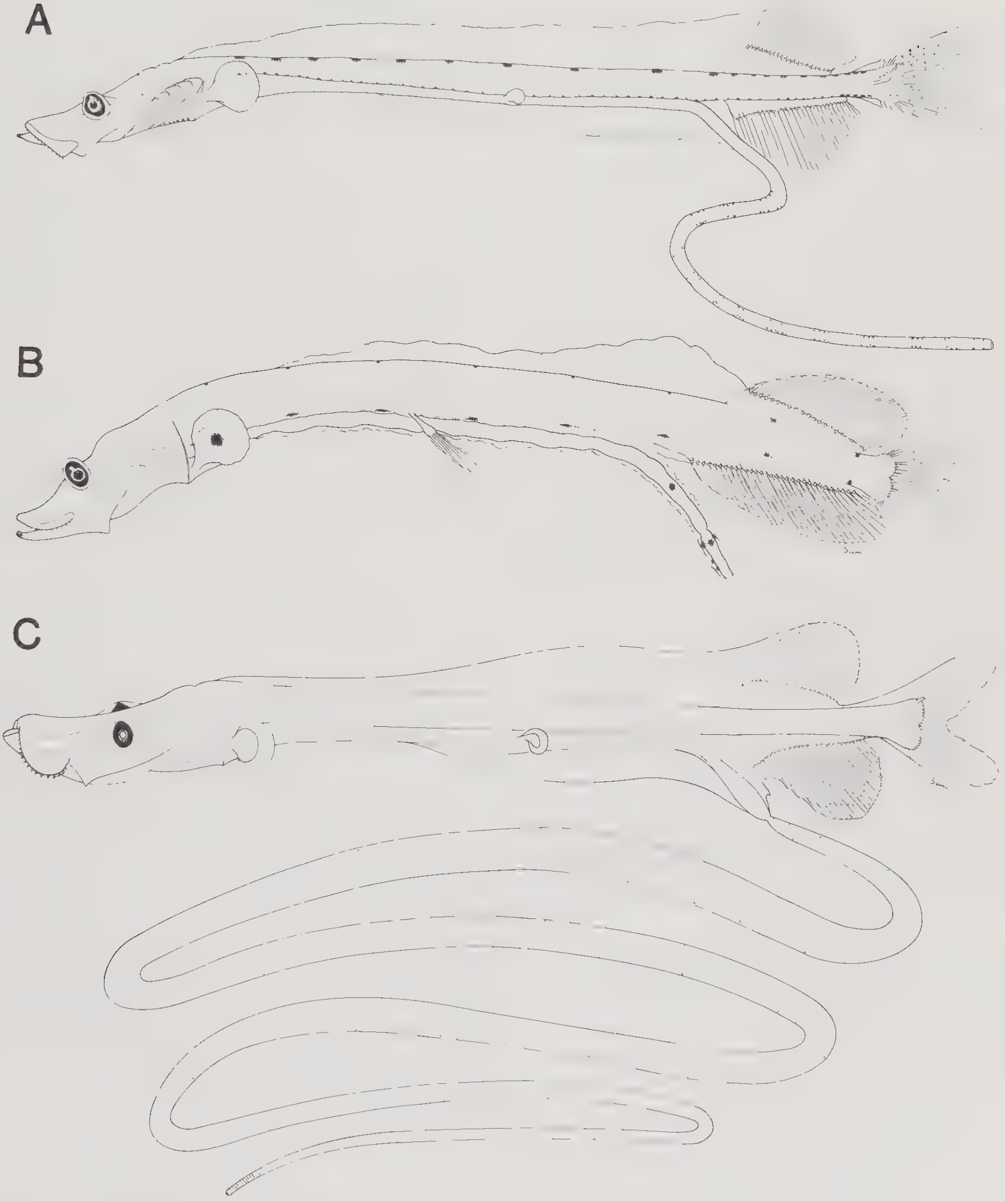

Fig. 93. Larvae of Malacosteidae. (A) *Aristostomias scintillans*, 34.7 mm, CalCOFI 5008 Sta. 70.30; (B) *Photostomias* sp., 26.7 mm, ORI KH 73-5 Sta. 55-13, Bn 24-12; (C) Malacosteidae, 34.5 mm, from Moser (1981).

←

Fig. 92. Larvae of Melanostomiatidae. (A) *Bathophilus flemingi*, 25.5 mm, CalCOFI 4910, Sta. 80.137; (B) *B. brevis*, 15.7 mm, ORI KH 81-1, Sta. 17; (C) *B. nigerrimus*, 21.7 mm, redrawn from Sanzo (1931d); (D) *Eustomias* sp. 33 mm, redrawn from Regan (1916).

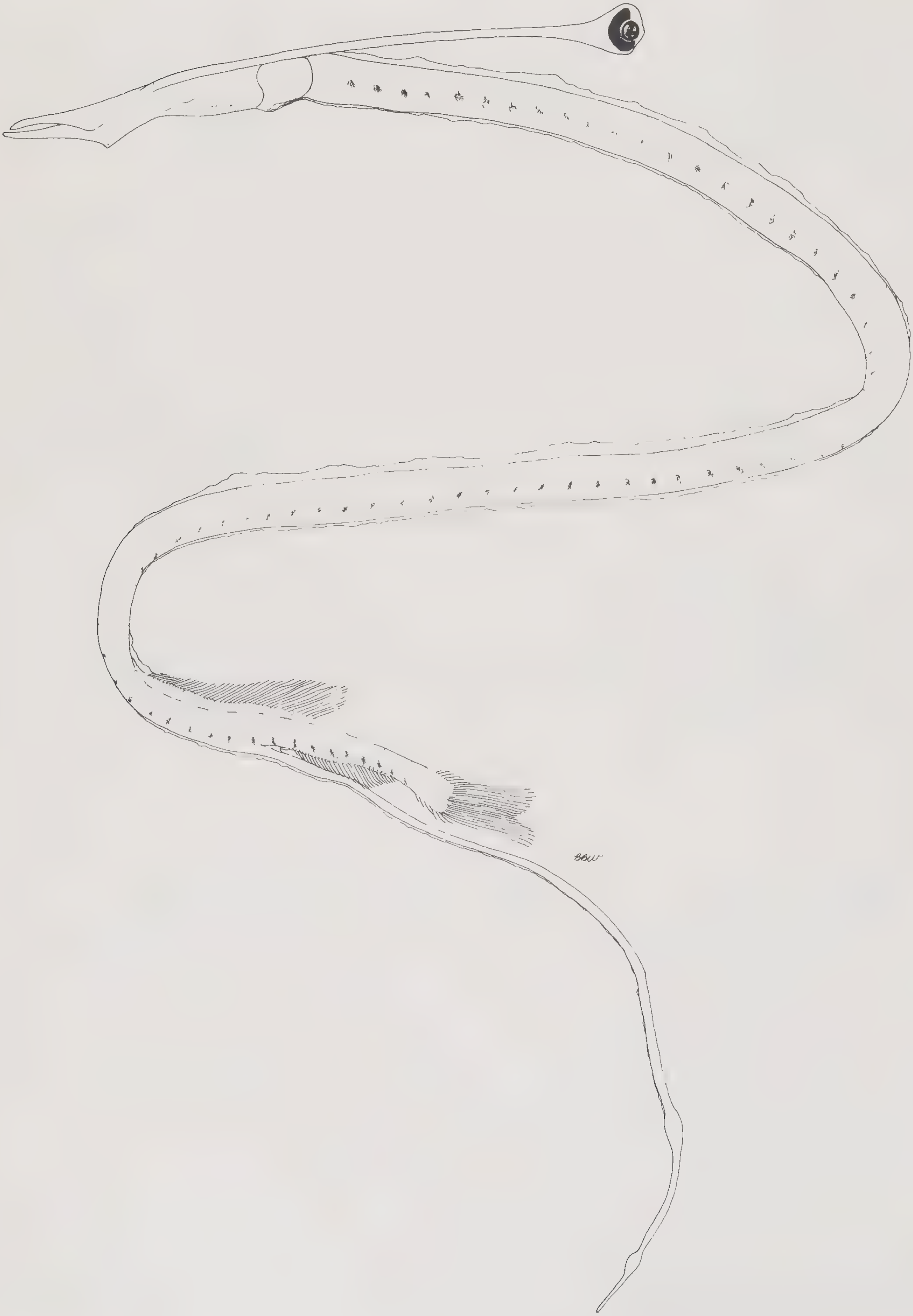

Fig. 94. Larva of *Idiacanthus antrostomus*, 55 mm, CalCOFI 6207 Sta. 90.120.

pairs and increasing in numbers with development to cover the entire dorsum; paired ventral series develop, initially posteriorly, and increase in numbers so that all myomeres have melanophores on the ventral surface; pigment on brain, snout, lower jaw, gular-isthmus region, otic region, caudal fin, and in vague rings along trailing gut. *Aristostomias* larvae were identified initially by E. H. Ahlstrom.

Photostomias guernei (Fig. 93B).—larvae reach about 30 mm; morphology similar to *A. scintillans* except eyes smaller and narrower and pelvic fins somewhat elongate; body pigment consists of a series of 8 minute dorsal melanophore pairs and 8 slightly larger opposing pairs along the ventral surfaces of the myomeres; melanophores at lower jaw symphysis, large melanophore on each pectoral fin base, sparse melanistic rings along trailing gut.

Malacosteid C (Fig. 93C).—intact specimen (captured by Dr. Richard Harbison, WHOI) has morphological and meristic characters of malacosteid larvae but lacks pigment except on the extensive gut. Shallow capture locality of this specimen and our capture of large *A. scintillans* larvae in MANTA nets indicates late-stage malacosteid larvae have a shallow distribution in the water column.

Idiacanthidae (Fig. 94).—Brauer (1906, 1908) described the remarkable larvae of *Idiacanthus* and named them *Stylophthalmus paradoxus.* Beebe (1934) correctly identified the larvae and described them in detail. *Idiacanthus* larvae are extremely slender, reaching a length of 35–70 mm depending on the species. Other characteristics are: elongate and extremely flat head; elliptical eyes on long stalks with cartilaginous supporting rods; stalk length up to 27% of body length in *I. antrostomus* (Weihs and Moser, 1981); gut slender, deflected at anal fin origin and trailing; finfold small; dorsal fin begins forming in preflexion larvae; dorsal fin larger than anal fin and slightly in advance of it in postflexion larvae; during transformation, rays added sequentially anteriad so that in adults the dorsal extends about ⅔ of the body length and the anal about ⅓; pectoral fins well developed but lost at transformation and pelvic fins develop in transforming females, but not at all in males; pigment pattern consists of a melanophore on the posterior margin of each hypaxial myomere, spreading into the myosepta when expanded, several elongate internal blotches in the isthmus region, and a series of melanophores along the trailing gut; adult males of *I. fasciola* reach 32–42 mm SL, lack teeth and paired fins and have relatively larger eyes and an enormous luminous gland.

RELATIONSHIPS

Information on larval characters of 18 of the 26 stomiatoid genera recognized by Fink (this volume), representing all 6 of the families recognized by Weitzman (1974), permits some preliminary generalizations and conclusions: (1) Larvae of Stomiatidae and Chauliodontidae are similar in morphology and are distinct from other stomiatoids. Pigmentation provides further evidence of this; *Chauliodus* larvae are unique among known stomiatoids in lacking pigment after the yolk-sac stage and the median series of gut melanophores of *Stomias* also appear to be unique. (2) Larvae of Astronesthidae are diverse in morphology and pigmentation and most of the larval specializations that appear in other stomiatoid families are found among astronesthid genera. Larval specializations of some genera (e.g., ornamented trailing gut, trailing gut deflected at mid-body, rudder-like finfolds) are not found elsewhere in Stomiatoidea. Heterogeneity of larval characters in Astronesthidae supports Fink's view that the group is paraphyletic. (3) In the Melanostomiatidae, larvae of *Melanostomias, Photonectes, Echiostoma, Opostomias, Flagellostomias, Odontostomias* and *Leptostomias* are similar in morphology, have paired melanophore series on the dorsum, and differ chiefly in head size, body depth, and in the extent of myosepta pigment. *Tactostoma* larvae have the characters of this group of genera except that the body is extremely slender and the pigmentation is lost in the postflexion stage. Larvae of *Bathophilus* differ from those of the above group in a number of characters (voluminous gut with specialized terminal section, melanophore series on the ventral surface of the myomeres, lack of myosepta pigment). Larvae of *Eustomias* are different from all known larvae of Melanostomiatidae in having a trailing gut, flat head and snout, and a pigment pattern consisting of a median series of up to 11 large melanophores on the dorsum. Except for this latter feature, *Eustomias* larvae are similar to those of Malacosteidae. (4) *Idiacanthus* larvae have a combination of characters unique among stomiatoids. The stalked eyes are autapomorphic. Larval characters provide no support for Fink's hypothesis that this genus is closely related to *Tactostoma.*

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8446

Capturing and Restraining Technique for Experimental Work on Small Tuna in Large Laboratory Holding Tanks

Our recent studies on induced spawning of captive tuna at the Kewalo Research Facility (National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory) have required new methods of handling these fish and minimizing injury. Since our procedures (Kaya et al. 1981; 1982) involve periodic gonadal biopsies of live fish, as described by Shehadeh et al. (1973) the fish must be kept immobile while gonadal tissue is extracted by a catheter inserted into the urogenital aperture. Such procedures must be effected without traumatizing the fish seriously enough to prevent their subsequent spawning. The tunas used in this experiment were kawakawa (*Euthynnus affinis*) and skipjack (*Euthynnus pelamis*) 40 to 50 cm (15.7 to 19.7 inches) in length and 1.2 to 3.2 kg (2.6 to 7.0 lb) in weight. They were held in groups of up to 20 in 7.3 m (24 ft) diameter by 1.1 m (3.6 ft) deep holding tanks. Fast and powerful, these fish are difficult to capture from holding tanks and to physically restrain them for any manipulative purposes usually causes serious and often fatal harm. Lacking protective scales on their skins, the fish are readily bruised by any but the most gentle contact and their caudal fins are easily frayed. Attempts to restrain them often produce internal injuries which may result in death within a few days, and survivors are prone to develop an apparently stress-related condition referred to as "puffy snout." This condition obviates their usefulness as experimental specimens and is eventually fatal.

Preliminary experimentation eliminated the use of anesthesia as a satisfactory approach for working with more than a few tuna at a time. The fish can be injured by handling associated with the administration of an anesthetic. In addition, as obligatory ram ventilators they must pass water over their gills by moving forward with their mouths open. Tunas anesthetized deeply enough for the biopsy procedure must then be nursed until they are capable of coordinated swimming. This process is time consuming and increases handling of each specimen.

To capture these fish from holding tanks and manipulate them with minimal injury, we developed procedures to: (1) prevent contact between fish and abrasive surfaces during the capture and biopsy processes; (2) immobilize each fish sufficiently to effect the catheterization; (3) permit rapid processing of each specimen; and (4) allow the sequential handling of every specimen in a holding tank.

The capture system (Fig. 1) was designed to force a fish to swim into a transparent capture sac. The capture sac was made from transparent polyethylene sheeting, 0.15 to 0.25 mm (6 to 10 mils) thick, cut to size and shape and

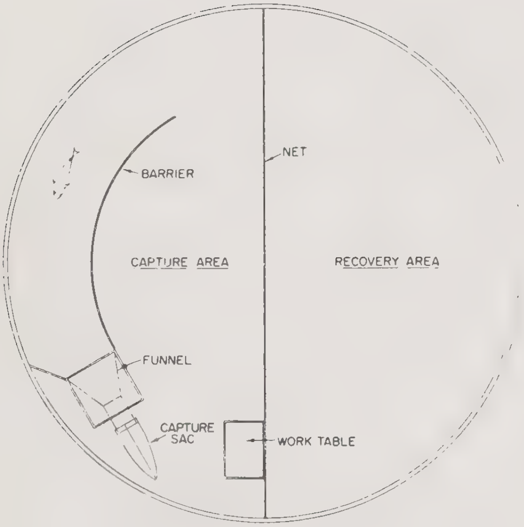

Fig. 1. Capture system.

heat-sealed along the edges (Audion Electronics[1] sealer obtained from Packaging Aids Corp.[1], 469 Bryant Street, San Francisco). Dimensions of the capture sacs were determined by constructing prototypes around similar-sized, dead specimens obtained from commercial sources. A tapered enclosure was formed between the plastic-lined wall of the holding tank and a portable curved barrier. The enclosure led into a funneling chamber which terminated at the capture sac. The barrier measured 0.60 × 3.05 m (2 × 10 ft) and was made of opaque polyethylene sheeting attached around a rigid polyvinyl chloride (PVC) pipe frame. The frame was bent to conform to the curvature of the tank (Fig. 1), by the inclusion of 45° elbows along its length. The funneling chamber (Fig. 2) had a 0.61 × 0.61 × 0.91 m (2.0 × 2.0 × 3.0 ft) long frame supporting a cone constructed of vinyl-coated nylon fabric (Herculite[1], available at sail, awning, or canvas retailers). The narrow, distal end of the cone was attached to a rigid polyethylene cylinder 0.3 m (1.0 ft) in diameter, made by removing the bottom from a bucket.

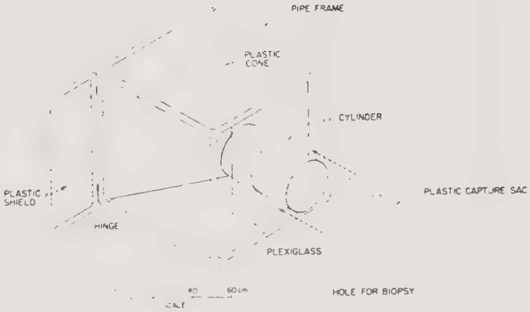

Fig. 2. Funneling chamber.

To capture fish from a holding tank, water was drawn down to a depth of about 0.6 m (2.0 ft) and the tank was divided in half with a seine (Fig. 1) All specimens were originally retained in the "capture" half. One person held the capture sac with its opening over the distal end of the funneling chamber while another used a small seine to isolate a specimen within the enclosure and forced it to swim through the funneling chamber into the capture sac. The opacity of the walls of the enclosure and the funneling cone tended to deter fish from ramming into them, and the flexible materials minimized injury when accidental contact was made. Fish generally made a dash to attempt escape through the apparently open end of the cylinder and swam into the capture sac. To lift a fish onto the restraining table (Fig. 3), the capture sac was grasped along the seamed side close to the body of the fish, and sac and enclosed fish were swung to the table in a fast, continuous motion. Grasping along the seamed side prevented tearing open of the seam from the fish's weight.

The restraining device consisted of a table padded with a layer of foam rubber and to which two strips of foam rubber and a sheet of opaque, vinyl-coated fabric (Herculite[1]) were attached along one edge (Fig. 3A). The fish, still contained within the capture sac, was placed on the padded surface and the two strips of foam were folded over its head and caudal fin. The plasticized sheet was then drawn down tightly over the fish and held in place with Velcro[1] strips (Fig. 3B). The fish was thus tightly sandwiched between layers of foam rubber and soft plastic material. Movement of the fish was minimized by this re-

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[1] Reference to trade names or commercial sources does not imply endorsement by the National Marine Fisheries Service, NOAA.

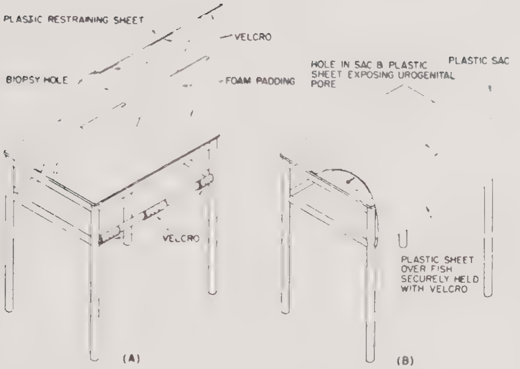
PLASTIC RESTRAINING SHEET
VELCRO
BIOPSY HOLE
FOAM PADDING
VELCRO
(A)
HOLE IN SAC & PLASTIC SHEET EXPOSING UROGENITAL PORE
PLASTIC SAC
PLASTIC SHEET OVER FISH SECURELY HELD WITH VELCRO
(B)

Fig. 3. (A) Restraining table. (B) Positioning of fish for gonadal biopsy.

straint and probably also by having its eyes covered by opaque material. The catheter could then be inserted through openings located in the restraining plasticized sheet and the capture sac (Fig. 3B). After processing, the fish was released into the "recovery" half of the tank and the procedure repeated on the remaining specimens in the "capture" half. To release a fish, the transfer procedure earlier described was reversed and the capture sac pulled free as the specimen was immersed.

This system allowed rapid, efficient processing of specimens with minimal trauma to the fish and with practice, procedure from catheterization to release could be executed in less than 20 seconds. When biopsied in the morning, our captive tuna often resumed feeding by the afternoon of the same day. Two groups of captive kawakawa survived monthly biopsies of 18 and 19 months in a program to monitor their gonadal maturation. Selected individuals have been successfully subjected to multiple biopsies within 48-hour periods during induced spawning trials (Kaya et al. 1981).

Although developed originally for gonadal biopsies of tuna, the system can be used on other fishes and can be modified for other purposes. We have used it successfully on jacks (*Caranx* sp.) and dolphinfish (*Coryphaena hippurus*). A second opening, not depicted in Fig. 3B, is made in the restraining sheet and capture sac to allow access to a selected area on the dorsal surface of restrained specimens. This second opening is used to place identifying marks on individuals, using the silver nitrate technique described by Thomas (1975), or to administer hormone injections.

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8447

Early Life History Stages of Fishes and Their Characters

A. W. KENDALL, JR., E. H. AHLSTROM AND H. G. MOSER

PATTERNS OF TELEOST EARLY LIFE HISTORY

IN discovering that Atlantic cod lay free-floating planktonic eggs which develop into pelagic larvae, G. O. Sars, in 1865 (see Hempel, 1979; Ahlstrom and Moser, 1981) had also come upon an example of the widespread life history pattern of marine fishes. Most marine fishes, regardless of systematic affinities, demersal or pelagic habits, coastal or oceanic distribution, tropical or boreal ranges, spawn pelagic eggs that are fertilized externally and float individually near the surface of the sea (Fig. 5). These eggs range from about 0.6 to 4.0 mm in diameter (mode about 1 mm) and generally are spherical. Within a species there is little variation in egg characters such as size, number and size of oil globules, and pigmentation and morphology of the developing embryo. Development time is highly temperature dependent and also species-specific. The eggs hatch into relatively undeveloped yolk-sac larvae which swim feebly and rely on their yolk for nourishment while their sensory, circulatory, muscular, and digestive systems develop to the point that they can feed on plankton. Even these yolk-sac larvae have characters (pigment patterns, body size and shape, myomere number) that reflect their heritage. After the yolk is utilized, they develop transient "larval" characters such as pigment patterns and, in some, specialized head spines and fin structures that are apparently adaptive for this phase of their life history. During this period more characteristics of the adult (e.g., meristic characters) gradually develop. At the end of the larval stage, they may go through an abrupt transformation to the juvenile stage, particularly if they move from a pelagic to demersal habitat, or the transformation may be gradual. In some fishes, there is a prolonged and specialized stage between the larval and juvenile stages. These pelagic (often neustonic) forms eventually transform into demersal juveniles. The juvenile stage is characterized by specimens having the appearance of small adults—all fin rays and scales are formed, the skeleton is almost

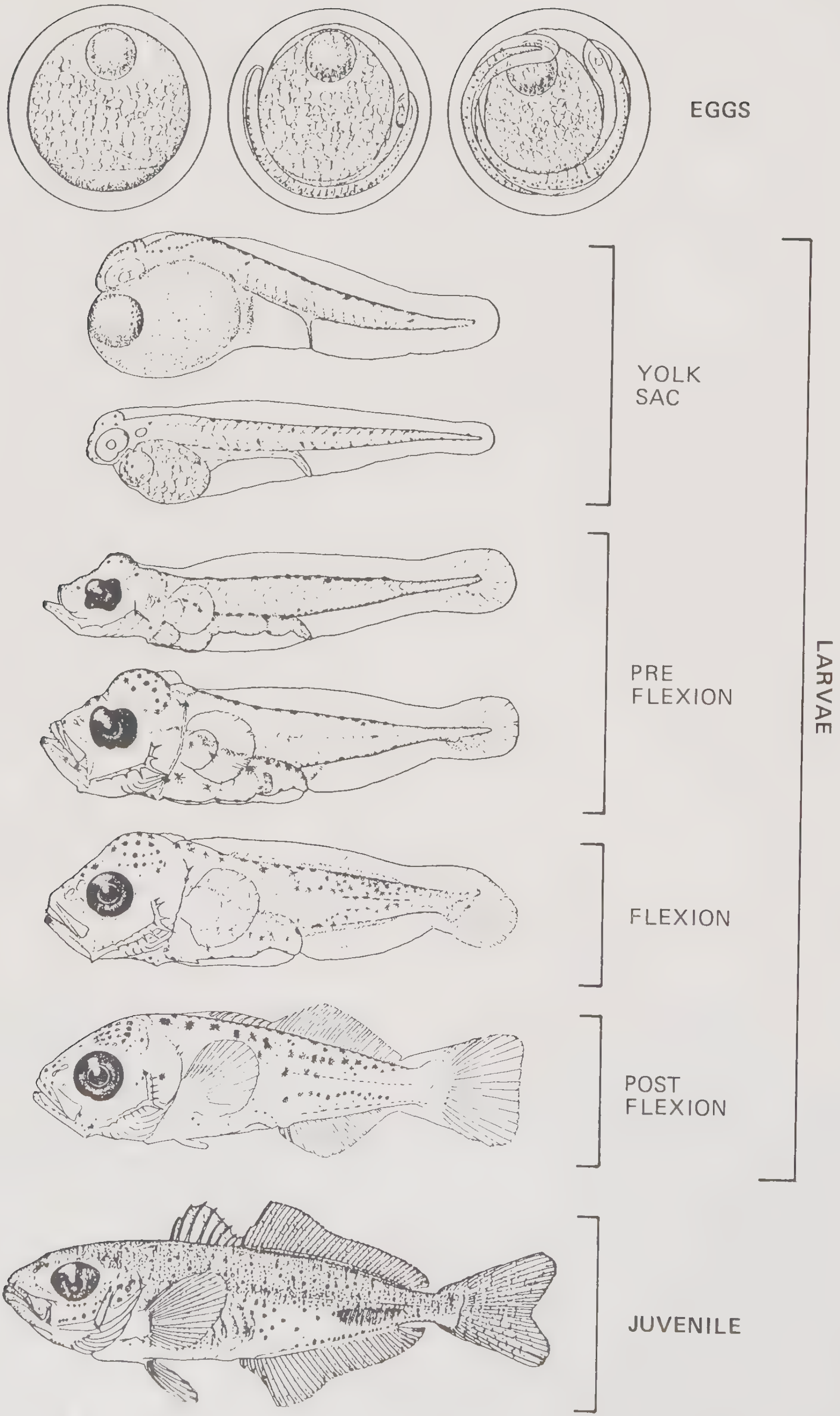

EGGS
YOLK SAC
PRE FLEXION
FLEXION
POST FLEXION
LARVAE
JUVENILE

Fig. 5. Early life history stages of *Trachurus symmetricus* from Ahlstrom and Ball (1954).

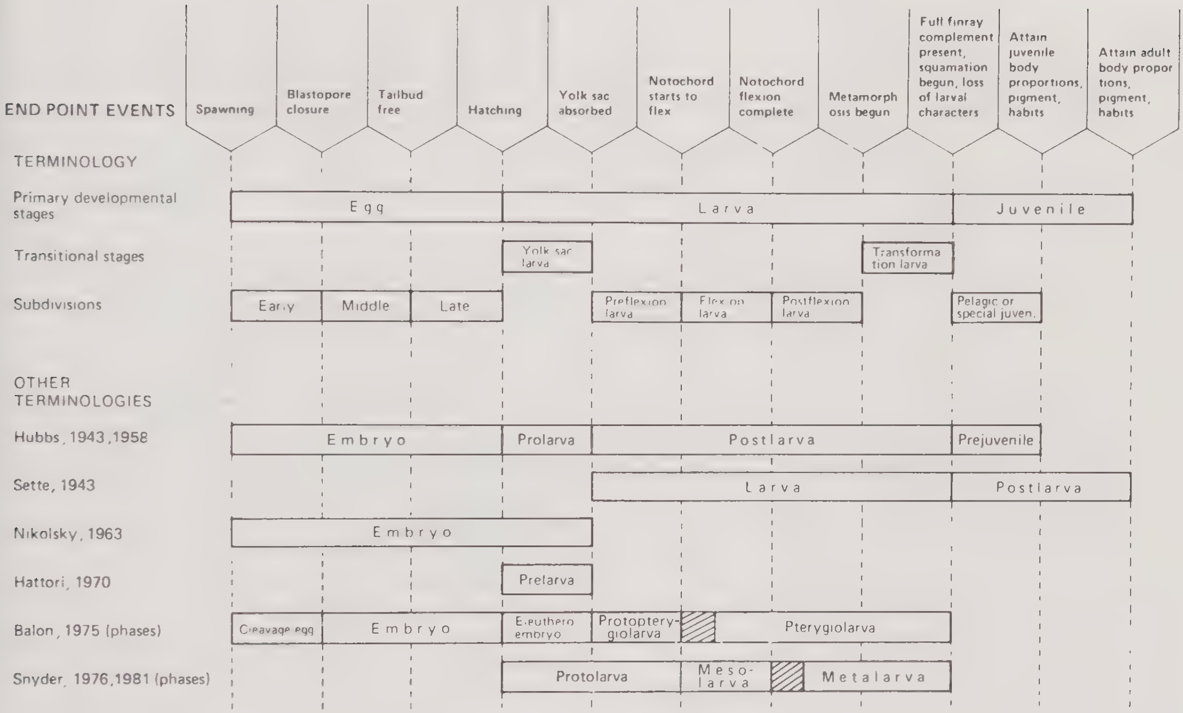

END POINT EVENTS
Spawning
Blastopore closure
Tailbud free
Hatching
Yolk sac absorbed
Notochord starts to flex
Notochord flexion complete
Metamorphosis begun
Full finray complement present, squamation begun, loss of larval characters
Attain juvenile body proportions, pigment, habits
Attain adult body proportions, pigment, habits
TERMINOLOGY
Primary developmental stages
Egg
Larva
Juvenile
Transitional stages
Yolk sac larva
Transformation larva
Subdivisions
Early
Middle
Late
Preflexion larva
Flexion larva
Postflexion larva
Pelagic or special juven.
OTHER TERMINOLOGIES
Hubbs, 1943,1958
Embryo
Prolarva
Postlarva
Prejuvenile
Sette, 1943
Larva
Postlarva
Nikolsky, 1963
Embryo
Hattori, 1970
Prelarva
Balon, 1975 (phases)
Cleavage egg
Embryo
Eleuthero embryo
Protopterygiolarva
Pterygiolarva
Snyder, 1976,1981 (phases)
Protolarva
Mesolarva
Metalarva

Fig. 6. Terminology of early life history stages.

completely ossified, the larval pigment pattern is overgrown or lost and replaced by dermal pigment similar to that of the adults, and the body shape approximates that of the adults.

Although this is the most frequently observed life history pattern, there are many variations (see Breder and Rosen, 1966) often related to increased parental investment in individual progeny with a concomitant decrease in fecundity and larval specializations. There is scant information on the young of many deep-sea fishes, and this may be due in part to life history strategies that do not include eggs and larvae that occur in the epipelagic zone (where most of the collecting is done). Marshall (1953) discussed life history adaptations of these fish such as the production of few, large yolky eggs that hatch into relatively advanced larvae. These young may remain far below the more productive surface layers, and thus not be susceptible to most sampling procedures. Markle and Wenner (1979) cite evidence for demersal spawning of two species of groups (Alepocephalidae, Zoarcidae) that are seldom collected in the plankton as larvae.

Many coastal marine and nearly all freshwater fishes lay demersal eggs which are generally larger than the 1 mm mode of pelagic eggs. In such fish development from hatching through juvenile stage is direct and the larvae gradually attain adult characters of shape, pigmentation, and meristic features. The demersal eggs frequently are adhesive and laid in some sort of nest. Parental care of the nest is observed in many species, and this care may extend to the larvae after hatching (e.g., mouth brooding in cichlids, ariids). Parental care takes another form in *Sebastes,* where development through the yolk-sac stage takes place in the ovary and first-feeding larvae are extruded. Viviparity, in which nourishment is supplied by maternal structures, has evolved many times (e.g., poeciliids, some zoarcids, embiotocids), whereby the larval stage is bypassed and the fish are extruded ("born") as juveniles (Wourms, 1981).

EARLY LIFE HISTORY STAGES

Between spawning and recruitment into the adult population, most fishes undergo dramatic changes in morphology and hab-

TABLE 2. EXAMPLES OF CHARACTERS OF PELAGIC EGGS THAT MAY BE USEFUL FOR SYSTEMATIC STUDIES OF CERTAIN FISHES.

Character	Character states	Systematic groups
Egg size	<1 mm–>5 mm >3 mm–>5 mm	Pleuronectidae Anguilliformes
Egg shape	Round—oblong	Engraulidae Ostraciontidae
Envelope sculpturing	Varying distances between pores Varying length/density of filaments	Gadidae Atheriniformes (Exocoetidae)
Oil globule position	Anterior to posterior in yolk sac	Perciformes
Embryonic characters	State of development of various organs/organ systems at various developmental mileposts	Gadidae

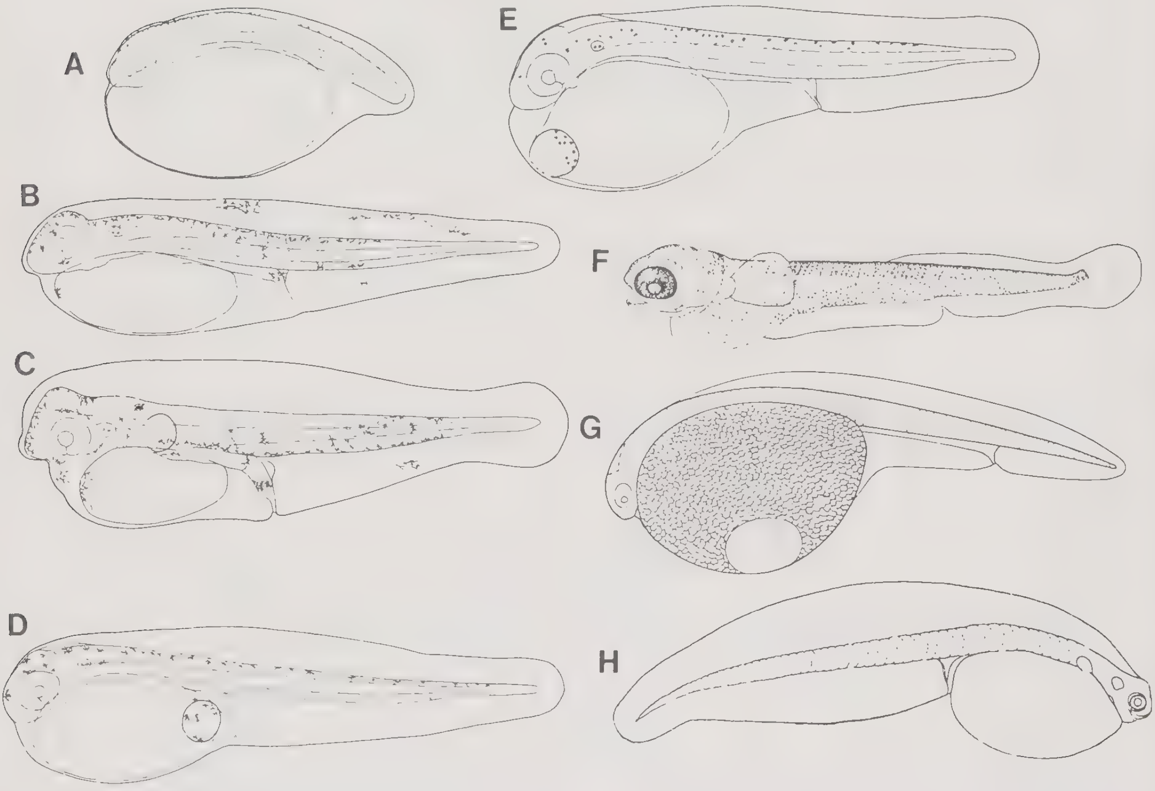


Fig. 7. Examples of features of yolk-sac larvae of teleosts. (A–C). *Paracallionymus costatus.* A. soon after hatching 0.98 mm NL; B. 1.8 mm NL; C. 1.9 mm NL. From Brownell (1979). Features demonstrated in: (A) include the small size of the larva, the lack of an oil globule, the segmented yolk, and the dorsally arranged melanophores; (B) demonstrates the migration of melanophores ventrally and the formation of the anus producing a preanal finfold; (C) demonstrates further ventral migration of melanophores, beginning of larval pectoral fin formation, the decrease in yolk-sac size, and beginning of pigment in the eye; (D) *Diplodus sargus.* 2.4 mm NL. From Brownell (1979). Single pigmented oil globule posterior in the unsegmented yolk and a short preanal finfold are demonstrated; (E) *Trachurus t. capensis.* 2.2 mm NL. From Brownell (1979). Single pigmented oil globule anterior in segmented yolk with moderately long preanal finfold demonstrated; (F) *Cololabis saira.* 5.1 mm SL. (original). Well-developed, heavily pigmented yolk-sac larva at hatching with notochord flexion beginning and some caudal rays formed; (G) *Argentina silus.* 7.7 mm. Redrawn from Schmidt (1906c). A large but poorly developed yolk-sac larva at hatching with a large oil globule; and (H) *Hippoglossus stenolepis.* 9.5 mm. From Pertseva-Ostroumova (1961). A large but poorly developed yolk-sac larva at hatching with no oil globule.

its. As mentioned earlier, at hatching, particularly in marine fishes with pelagic eggs, the fish is in an extremely undeveloped state and then, as a free-living individual, it gradually develops the adult characters. This process is continuous, but there are morphological and ecological mileposts that are significant in the life of the fish and which allow us to subdivide this process so that we can communicate results of our studies and compare different fishes at the same moment in development.

Fish early life history has been and continues to be studied from a number of different perspectives (Ahlstrom and Moser, 1976). Some studies deal directly with embryology and later ontogeny, others emphasize functional morphology of larval structures, apply larval features to taxonomic and systematic studies, investigate the ecology of eggs and larvae, or use these stages to address fishery-related problems such as assessment of spawning stock size and recruitment success. All of these studies have in common the need to subdivide early life history and communicate information based on processes and events occurring during these subdivisions. As with any communication, it is vitally important to use terms that are clearly defined and this is particularly true with the diverse disciplines that are involved in larval fish studies. Historically, several disciplines have used different names for the same stage, or subdivided development differently [see Okiyama (1979a) and Fig. 6 in this paper]. This has led to confusion rather than communication.

Several criteria seem appropriate for defining stages of development to be used by students of any discipline. The variety of developmental patterns should be recognized and the definitions should apply to as many patterns as possible. Thus, stages should be based on very widespread, fundamental features of development. The stages should have some significance in the life history of the fish, both morphologically and func-

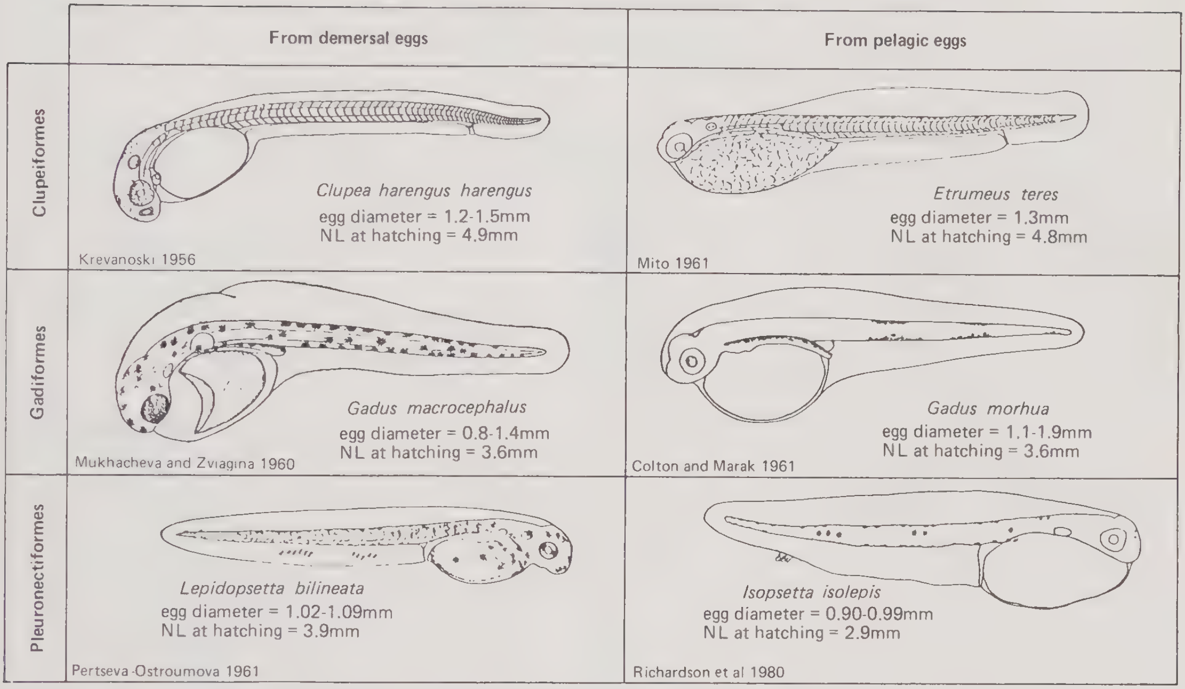

From demersal eggs
From pelagic eggs
Clupeiformes
Gadiformes
Pleuronectiformes
Clupea harengus harengus
egg diameter = 1.2-1.5mm
NL at hatching = 4.9mm
Krevanoski 1956
Etrumeus teres
egg diameter = 1.3mm
NL at hatching = 4.8mm
Mito 1961
Gadus macrocephalus
egg diameter = 0.8-1.4mm
NL at hatching = 3.6mm
Mukhacheva and Zviagina 1960
Gadus morhua
egg diameter = 1.1-1.9mm
NL at hatching = 3.6mm
Colton and Marak 1961
Lepidopsetta bilineata
egg diameter = 1.02-1.09mm
NL at hatching = 3.9mm
Pertseva-Ostroumova 1961
Isopsetta isolepis
egg diameter = 0.90-0.99mm
NL at hatching = 2.9mm
Richardson et al 1980

Fig. 8. Newly hatched yolk-sac larvae of related fishes with pelagic and demersal eggs of comparable sizes.

tionally, such as a particular type of nourishment or locomotion. Also the endpoints for the stages should be easily observed and sharply defined.

The most general scheme of terminology of early development of fishes includes (Fig. 5):

The "egg stage" (spawning to hatching). The egg stage is used in preference to the embryonic stage because there are characters present during this stage other than just embryonic characters (e.g., those associated with the egg envelope).

The "larval stage" (hatching to attainment of complete fin ray counts and beginning of squamation). One of the fundamental events in development of most fishes is the flexion of the notochord that accompanies the hypochordal development of the homocercal caudal fin. It is convenient to divide the larval stage on the basis of this feature into "preflexion," "flexion," and "postflexion" stages. The flexion stage in many fishes is accompanied by rapid development of fin rays, change in body shape, change in locomotive ability, and feeding techniques.

The "juvenile stage" (completion of fin ray counts and beginning of squamation until fish enters adult population or attains sexual maturity).

Transitional stages can also be recognized: the "yolk-sac larval stage" (between hatching and yolk-sac absorption); and the "transformation stage" (between larva and juvenile). Metamorphosis occurs during this stage and is considered complete when the fish assumes the general features of the juvenile.

The life histories of some fishes include other specialized ontogenetic stages that have received various names. In some cases, these are the generic names under which these stages were described before they were recognized as larvae of other species (e.g., the leptocephalus stage of Anguilliformes, the scutatus stage of *Antennarius,* the vexillifer stage of Carapidae, and the kasidoron stage of *Gibberichthys*). In other cases, consistent features of development of a group permit useful subdivisions of stages (e.g., in leptocephali the engyodontic and euryodontic stages).

THE EGG STAGE

Hempel (1979) reviewed the egg stage relative to fisheries investigations. Ahlstrom and Moser (1980) presented a concise review of the range of characters observed in pelagic fish eggs, particularly those useful in identifying eggs in plankton samples. Sandknop and Matarese in this volume also discuss this subject in detail. The characters that have proven useful for egg identification include egg size and shape, size of perivitelline space, yolk diameter and character (homogeneous or segmented), number and size of oil globules, texture of the egg envelope (smooth or with protrusions), pigment on the yolk and embryo, and characters of the developing embryo (relative rate of development of various parts, body shape, number of somites) (Table 2).

The egg stage has been subdivided by a number of workers (e.g., Apstein, 1909). Fishery biologists need to determine the age of eggs at the time of collection for production, drift, and mortality estimates. Embryologists have designated stages to coincide with significant developmental features. While the stages of fishery biologists are designed to divide the embryonic stage into several easily recognized portions, embryologists are more

TABLE 3. EXAMPLES OF USE OF CHARACTERS OF EARLY LIFE HISTORY STAGES IN TAXONOMIC AND SYSTEMATIC STUDIES. X indicates range of stages and taxonomic levels at which characters vary. (X) indicates infrequent state.

Character	Developmental stage						Taxonomic level				References
		Larvae									
	Egg	Yolk-sac	Preflexion	Flexion	Postflexion	Transformation	Species	Genus	Family	Order	Keyed to Table 4
Meristic characters											
Fin spines/soft rays			(X)	X	X				(X)	X	20
Principal caudal rays			X	X	(X)				(X)	X	20, 29
Pelvic fin			(X)	X	X				(X)	X	2, 38
Dorsal/anal fin				X	X		X	X			1, 2, 11, 19, 24, 27, 39
Pectoral fin			(X)	X	X		X				11, 19, 24, 27, 39
Vertebrae				X	X		X	X	X		1, 2, 3, 5, 11, 15, 17, 19, 20, 25, 27, 28, 33, 34
Branchiostegals			X	X	(X)				(X)	X	27, 38
Gill rakers					X	X	X				19
Larval characters											
Body shape		X	X	X	X	X	X	X			2, 3, 4, 5, 10, 11, 13, 14, 19, 20, 23, 24, 25, 26, 27, 28, 29, 31*, 33, 37, 40
Snout shape			X	X	X		X	X			28, 33, 35, 36, 38
Pigment patterns	X	X	X	X	X	X	X	X	X	X	1, 2, 3, 4, 8, 9, 11, 13, 14, 15, 17, 19, 20, 21, 22, 25, 27, 28, 29, 33, 36, 38, 39, 40
Head spines			X	X	X		X	X	X	X	9, 11, 23, 24, 25, 27, 36, 38, 40
Fin ray elongation			X	X	X		X	X			1, 9, 14, 23, 27, 29, 33
Fin ray ornamentation			X	X	X			X			14, 27, 29
Fin ray serration				X	X			X			27
Finfold size/shape		X	X					X			8, 10, 14
Preanal finfold		X	X					X			36
Pectoral size shape			X	X	X			X			8, 14, 15, 33
Larval gut											
Shape		X	X	X	X			X			20, 33, 38, 39
Length		(X)	X	X	X			X			14, 20, 29, 33, 38
Larval eye											
Shape			X	X	X			X			8, 10, 14, 20, 33
Stalked			X	X	X			X			14, 20, 33
Choroid tissue			X	X	X		X				10, 14, 20
Migration						X				X	29
Other characters											
Egg characters	X						X	X			6, 19, 20, 30, 32
Osteological development			(X)	X	X	X		X	X	X	7, 16, 19, 23, 29, 33, 40
Scale formation				X	(X)	X	X				11, 27
Photophore formation					X	X	X	X			12, 14, 21
Size at developmental stage	X	X	X	X	X	X	X	X			10, 11, 22, 23, 29, 30, 39
Fin development sequence			(X)	X	X		X	X			13, 14, 20, 26, 27, 34

* Emphasis on oil globule placement in yolk-sac larvae.

interested in tracing the sequence of development. The embryologist's approach will probably provide more useful information for systematic investigations.

Although excellent, early descriptive work was done on teleost embryology (e.g. Wilson, 1891), comparative research on development needs to be done to allow an evaluation of its value to systematics, a subject that has proven so fruitful among invertebrates. It appears, from the characters that have been studied in greatest detail, that convergence may overshadow phyletically significant information. For instance, the egg envelope sculpturing on *Pleuronichthys*, a pleuronectiform, was found even on scanning electron microscope examination to be quite similar to that on *Synodus*, a myctophiform (Sumida et al., 1979). Phylogenetically diverse fishes often have round pelagic eggs, about 1 mm in diameter, with a single oil globule. Demersal eggs from equally diverse fishes are generally larger than 1 mm and develop a vitelline circulatory system. Yolk segmentation seems to be a character of more primitive fishes, but some carangids and other perciforms have yolks that are secondarily segmented in an evolutionary sense. Detailed studies are needed to sort out these and other features of the teleost egg and its embryonic development in a systematic context.

TABLE 4. SOME CONTRIBUTIONS IN WHICH ONTOGENETIC CHARACTERS HAVE BEEN USED TO EXAMINE SYSTEMATIC RELATIONSHIPS (UPDATED FROM AHLSTROM AND MOSER, 1981).

No.	References	Date	Group dealt with	Stages			Larval characters showing relationships			
				Egg	Larvae	Juv. ad.	Among species	Among genera	Among subfam. or families	Among orders
1, 3, 5	Ege, V.	1930, 53, 57	Paralepididae	–	+	±	X	X		
2	Bertelsen, E.	1951	Ceratioidei	–	+	+	X	X	X	
4	Bertelsen, E., and N. B. Marshall	1956	Miripinnati	–	+	±	X	X	X	
6	Pertseva-Ostroumova, T. A.	1961	Pleuronectidae	+	+	±	X	X		
7	Berry, F. H.	1964a	Mar. teleosts	–	+	–				X
8	Pertseva-Ostroumova, T. A.	1964	Myctophidae	–	+	–		X		
9	Gutherz, E. J.	1970	Bothidae	–	+	–		X		
10, 14	Moser, H. G., and E. H. Ahlstrom	1970, 74	Myctophidae	–	+	±	X	X	X	
11	Mead, G. W.	1972	Bramidae	–	+	+	X	X		
12	Ahlstrom, E. H.	1974	Sternoptychidae	–	+	±		X		
13	Johnson, R. K.	1974b	Scopelarchidae	–	+	+	X	X		
15	Okiyama, M.	1974a	Myctophiformes	–	+	–		X	X	
16	Potthoff, T.	1974	Scombridae	–	+	+	X			
17	Richards, W. J., and T. Potthoff	1974	Scombridae	–	+	±	X			
18	Aboussouan, A.	1975	Carangidae	–	+	–		X		
19	Ahlstrom, E. H., J. L. Butler, and B. Y. Sumida	1976	Stromateoidei	±	+	±	X	X	X	
20	Ahlstrom, E. H., and H. G. Moser	1976	Mar. teleosts	+	+	+				X
21	Ahlstrom, E. H., H. G. Moser, and M. J. O'Toole	1976	Myctophidae	–	+	+		X		
22	Bertelsen, E., G. Krefft, and N. B. Marshall	1976	Notosudidae	–	+	±	X	X		
23	Futch, C. R.	1977	Bothidae	–	+	–		X	X	
24	Moser, H. G., E. H. Ahlstrom, and E. Sandknop	1977	Scorpaenidae	–	+	±	X	X	X	
25	Okiyama, M., and S. Ueyanagi	1978	Scombridae	–	+	–		X	X	
26	Powles, H., and B. W. Stender	1978	Sciaenidae	–	+	±		X		
27	Kendall, A. W., Jr.	1979	Serranidae	–	+	+		X	X	
28	Ueyanagi, S., and M. Okiyama	1979	Scombridae, Istiophoridae	–	+	+		X		
29	Amaoka, K.	1979	Pleuronectiformes (in part)	–	+	–		X	X	
30	Dotsu, Y.	1979	Gobiidae	+	+	–		X		
31	Suzuki, K., and S. Hioki	1979a	Percoidei	±	+	–		X	X	
32	Mito, S.	1979a, b	Mar. teleosts	+	–	–		X	X	
33	Okiyama, M.	1979b	Myctophoidei	–	+	–			X	
34	Potthoff, T., W. J. Richards, and S. Ueyanagi	1980	Scombrolabracidae	–	+	+		X	X	
35	Zahuranec, B. J.	1980	Myctophidae (*Nannobrachium*)	–	+	+	X	X		
36, 37	Richardson, S. L.	1981a,c	Cottidae	–	+	+		X		
38	Washington, B. B.	1981	Cottidae	–	+		X	X		
39	Johnson, R. K.	1982	Scopelarchidae Evermannellidae	–	+	+	X	X	X	
40	Kendall, A. W., Jr., and B. Vinter	1984	Hexagrammidae	–	+	+	X	X		

THE YOLK-SAC LARVAL STAGE

At hatching, larvae can be at various states of development, dependent to a large degree on the size of the yolk (Fig. 7). Larvae from eggs with small yolks are less developed at hatching than those that hatch from eggs with larger yolks. Since the bulk of marine fish spawn eggs that are about 1 mm in diameter and have a narrow perivitelline space, the yolk is only slightly less than 1 mm. Larvae from such eggs generally lack a functional mouth, eye pigment, and differentiated fins. They possess a large yolk sac relative to the size of the larva which supplies nourishment while the larvae develop to become self-feeding. Newly hatched larvae from demersal eggs are generally further advanced in development than larvae from pelagic eggs of comparable size (Fig. 8). In these and other fish with large eggs, hatching may be delayed until the yolk sac is absorbed and the larvae are ready to feed at hatching, having bypassed the yolk-sac larval stage. The delayed absorption of yolk reaches an extreme in fishes such as salmonines in which the yolk-sac larva transforms directly into a juvenile; Hubbs (1943) proposed the term "alevin" be applied to this yolk-sac larval stage.

At hatching, locomotion and orientation of most yolk-sac larvae are aided by a continuous median finfold (dorsal, caudal, anal) and larval pectoral fins. During egg development, many fish embryos develop melanophores that originate in the neural

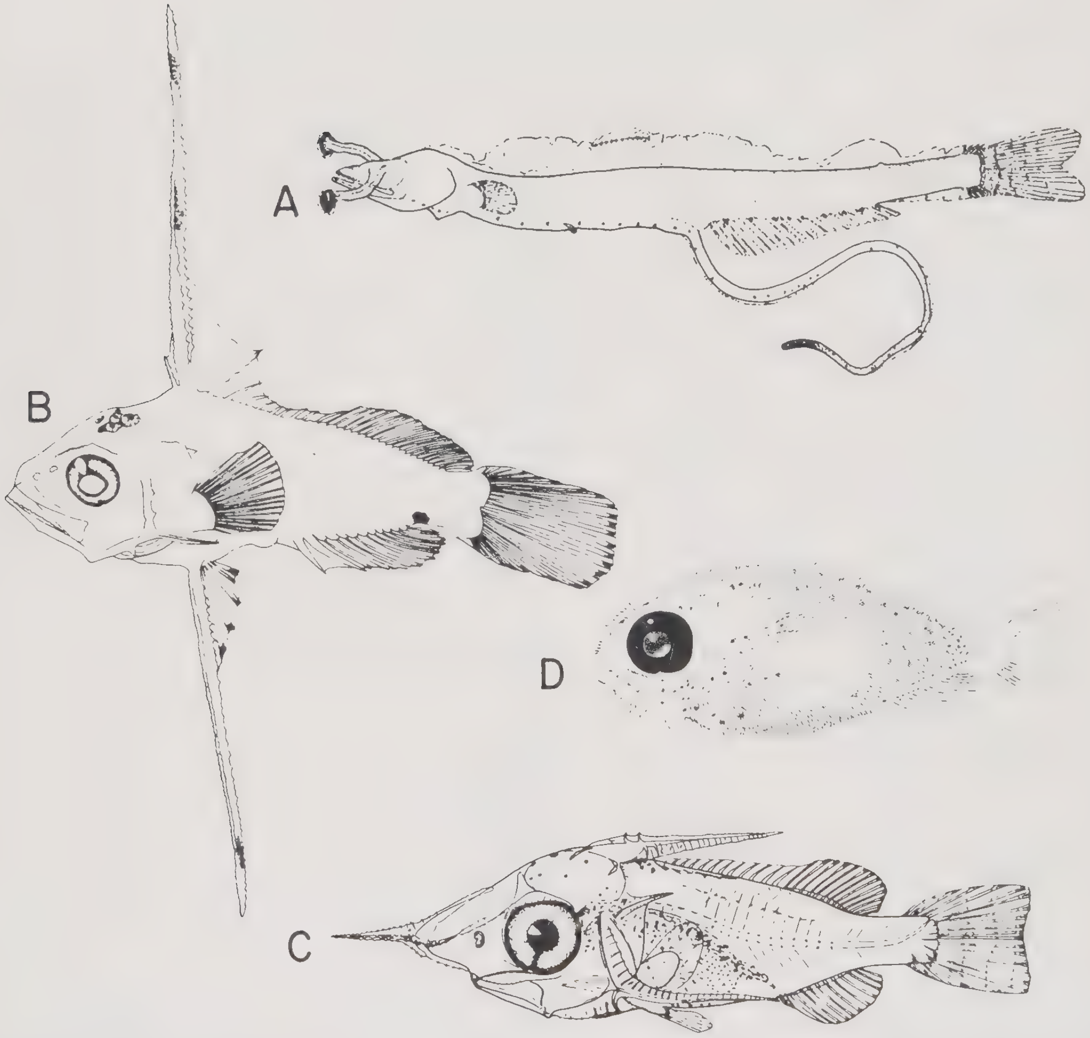


Fig. 9. Examples of teleost larvae illustrating extremes of some systematically useful larval characters. (A) *Myctophum aurolaternatum*, 26.0 mm (Moser and Ahlstrom, 1974). Note stalked oval eye with choroid tissue, trailing gut, and dorsal fin developing in finfold; (B) *Epinephelus* sp., 8.4 mm (Kendall, 1979). Note elongate, serrate dorsal and pelvic spines; (C) *Adioryx* (*Holocentrus*) *vexillarius*, 8.5 mm (McKenney, 1959). Note head spines; and (D) *Lopholatilus chamaeleonticeps*, 6.0 mm (Fahay and Berrien, 1981). Note spines on head and body.

crest and are generally aligned along the dorsal surface of the embryo. During the yolk-sac stage, these melanophores move laterally and ventrally to establish the beginning of the larval pigment pattern. Orton (1953a) describes these events in detail in *Sardinops sagax*. This realignment may begin during the late embryonic stages, before hatching. Some species hatch with few if any melanophores, and when they first appear, they are in ventral positions. Apparently, the pigment cells migrate before pigment formation occurs.

The presence and position of oil globules in yolk-sac larvae vary and can be of diagnostic value. In fishes with single oil globules, it can be far forward (e.g., labrids, most carangids, mullids, and lethrinids), in the middle of the yolk sac (e.g., some clupeids, serranids, and argentinids), or more usually near the rear of the yolk sac. The shape and relative size of the yolk sac itself are variable and provide additional taxonomic characters.

In summary, although the yolk-sac stage starts at hatching and ends when the yolk is absorbed, fish are at different stages of development with regard to such features as pigmentation, eye development, and fin formation during this stage. The striking pigment rearrangements that occur during this stage provide further emphasis that the yolk-sac stage is a transitional stage between the egg and larval stages.

THE LARVAL STAGE

During the larval stage many ontogenetic changes occur (Moser, 1981). Some of these relate directly to the development of the adult form while other changes and structures are specialized

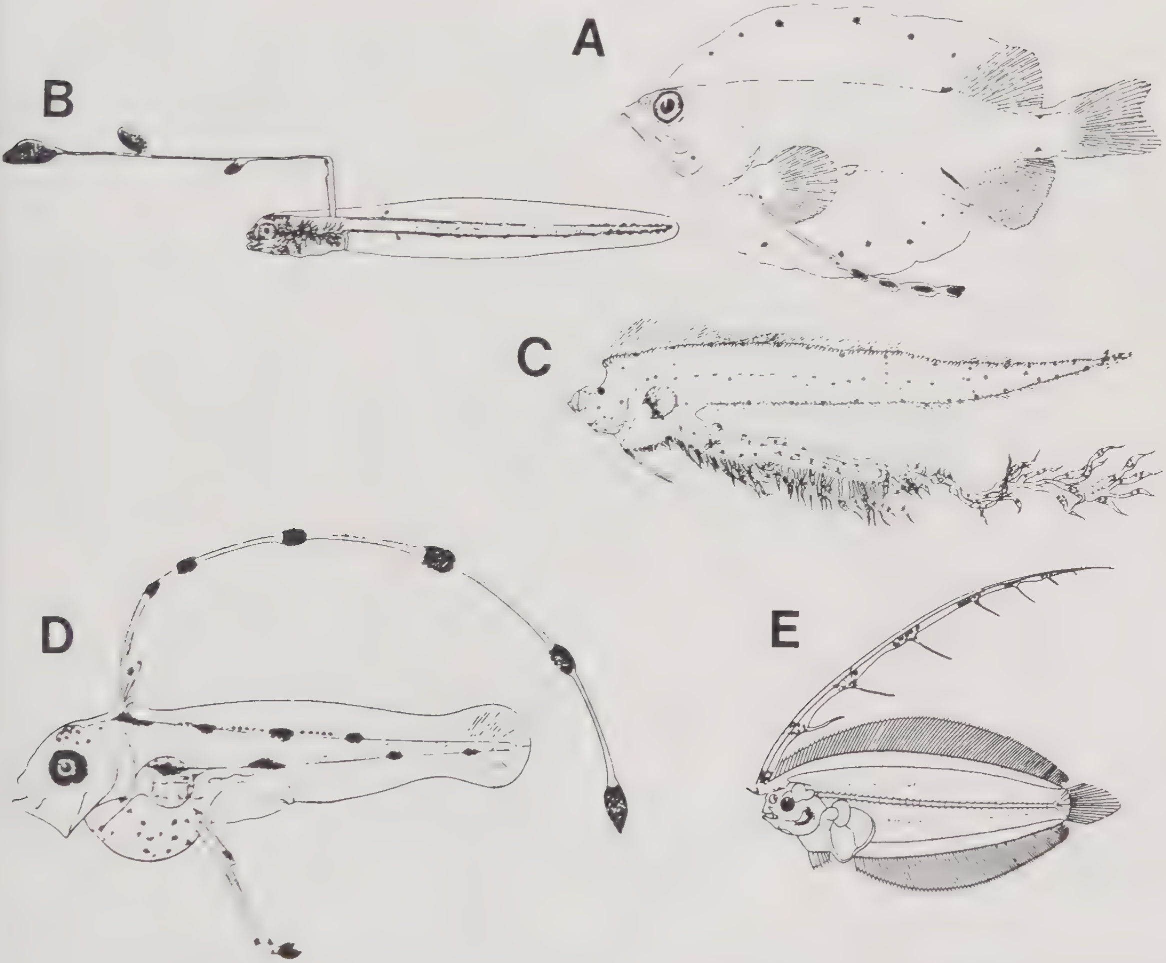


Fig. 10. Apparent convergence in siphonophore-mimicking appendages on larval fish. (A) *Loweina rara,* 17.6 mm. Note lower pectoral fin ray (Moser and Ahlstrom, 1970); (B) *Carapus* sp., 3.8 mm (Padoa, 1956j). Note elongate dorsal fin ray; (C) Exterilium larva, 64 mm. Note trailing gut (Moser, 1981); (D) *Lophotus* sp., 12.1 mm. Note elongate dorsal and pelvic ray (Sanzo, 1940); and (E) *Arnoglossus japonicus,* 30.5 mm. Note elongate dorsal ray (Amaoka, 1973).

and of presumed functional significance primarily for planktonic existence (Fig. 9). These latter features are of particular interest in systematic studies of larval fish ontogeny. They include pigment pattern, larval body shape, armature on head bones, and precocious (early forming), elongate, or serrate fin spines. The sequence and way of developing adult structures, such as the skeleton and fin rays, are also useful larval characters. All of the characters of the larvae—whether they are specialized larval characters or merely characters observable in the larvae—may have potential systematic value at some taxonomic level; however, the usefulness of most of the characters has not been evaluated (Tables 3 and 4).

Among the most taxonomically useful larval characters, generally at the specific or generic level, is the pigment pattern. Usually, each species has a distinct larval pigment pattern. In some the number and placement of individual melanophores are diagnostic, while in others the location, shape, and size of groups of melanophores are key characters. At a higher taxonomic level, in the myctophiforms for example, the peritoneal pigment blotches seem to indicate relationships on a suborder-family level. Problems associated with the usefulness of pigment patterns include 1) the widespread distribution of some patterns, and 2) the variable state of melanophore contraction on larvae of the same species. An example of the first problem is the frequent occurrence of a row of small melanophores along the ventral midline from just behind the anus to the tip of the tail. Another example is a pigmented area midlaterally on the caudal peduncle which occurs in numerous groups. A ventral spot at the junction of the cleithra is also quite common. These are just a few examples of widespread, presumably convergent pigment patterns that limit the usefulness of pigment in systematic studies of larvae. The causes for the observed differences in degree

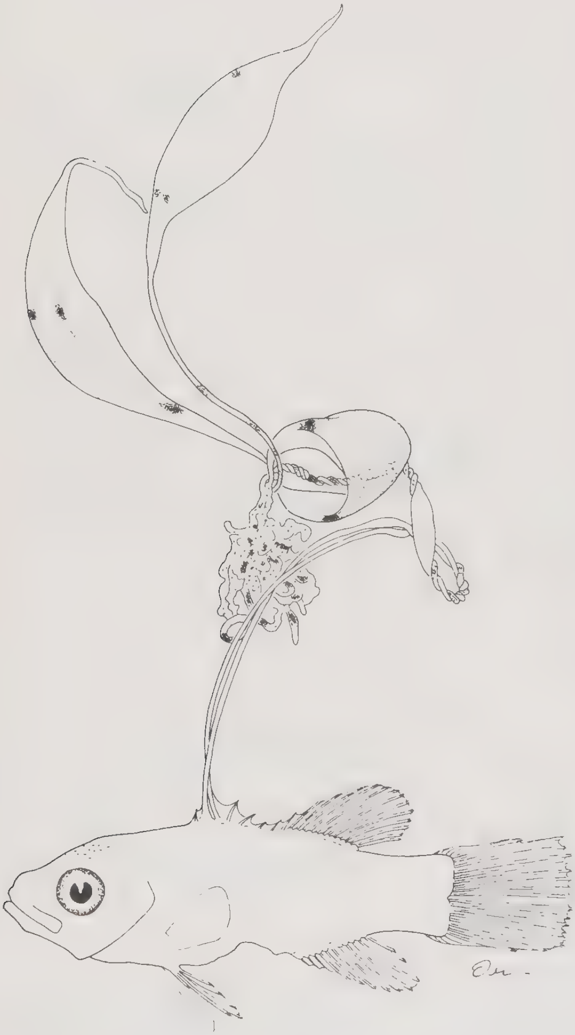


Fig. 11. *Liopropoma* sp., 11.0 mm. Collected by G. R. Harbison, 16 May 1981, 6°31.8′S, 150°21.8′E. Note elongate dorsal spines.

of contraction of melanophores are not well understood although they may be partially related to ambient light intensity. The relative size and placement of melanophores are genetically determined and therefore useful in a systematic context, while the degree of contraction seems to be physiologically determined.

In general, the body shape and size at various stages of development are characteristic of larvae at the generic or familial level, although subtle differences in body shape may be characteristic of species. Size at stage of development can be environmentally modified (e.g., by temperature or food) to some extent, but is primarily genetically determined. There appears to be some convergence in larval body shape, such as on a long tubular body in several divergent groups (e.g., Clupeiformes, Argentinidae, Blennioidea), just as there is on the "herring" morph of adults.

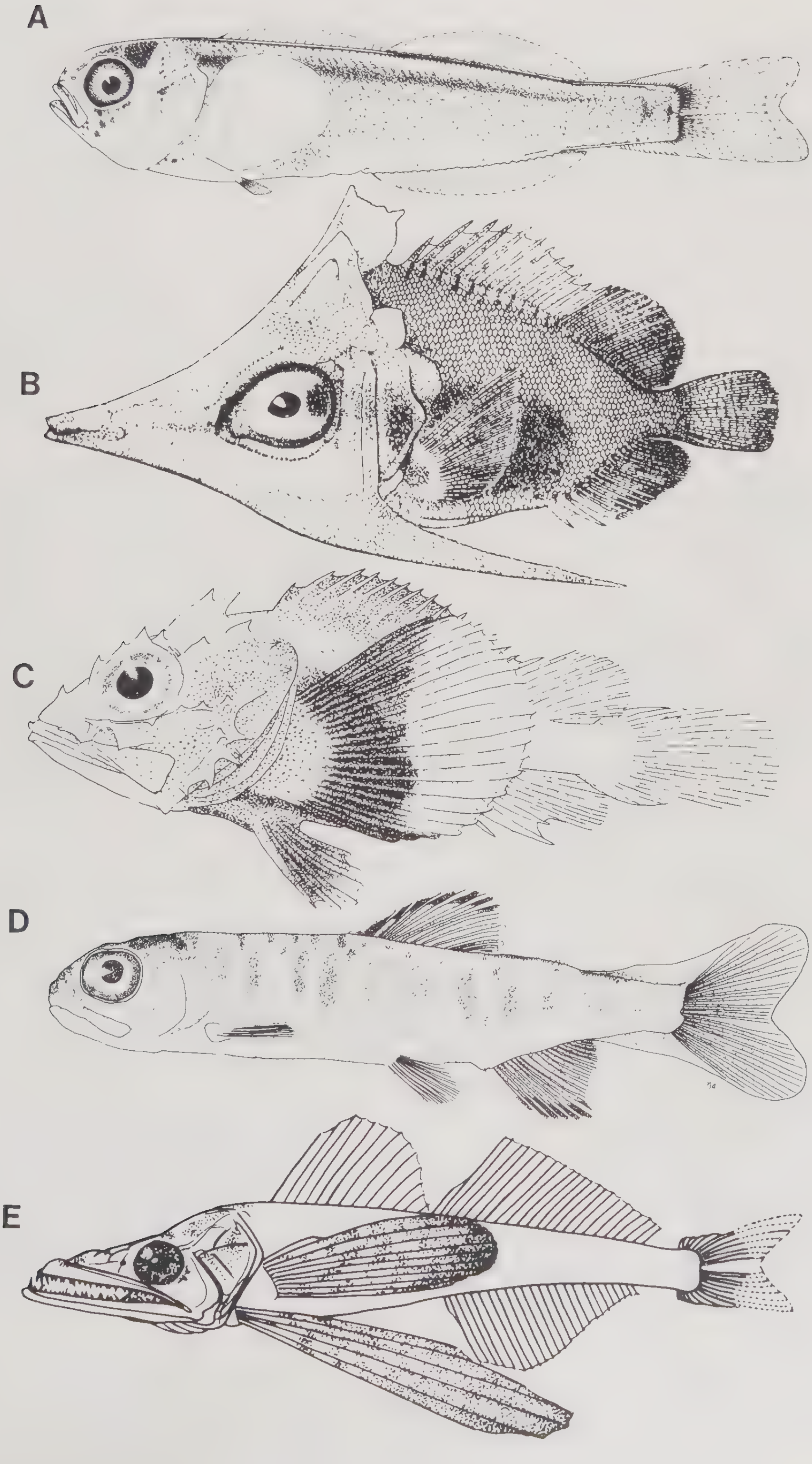
A valuable and fairly widespread set of larval characters concerns the development of spines and armature on bones of the head and cleithral region. Such armature has provided diagnostic larval characters as well as material for systematic inference at levels from species to order. Larval head armature appears to be a mark of the Acanthopterygii. Only a few scattered examples of such armature appear in fishes which have only soft rays as adults (e.g., *Sudis*). Within the spiny-rayed fishes, beryciforms are quite heavily armed with spines on many head bones. Perciforms usually do not have spines on the parietals but the supraoccipital is armed in some. The Scorpaeniformes are just the opposite: they tend to have head armature that includes spines on the parietals but do not have spines on the supraoccipital.

Nowhere are larval specializations more evident or varied than in the fins. Elongation of particular spines or soft rays or enlargement of whole fins are frequently seen. Such elongations have been described for rays of the dorsal, pelvic, pectoral, and caudal fins; thus they occur with both spines and soft rays. In some, these long rays may bear pigmented "bulbs" or appear like flagellae. Such specialized rays are produced in the dorsal, pectoral, or pelvic fins of taxonomically diverse fishes. The extended gut of "exterilium" ophidioid larvae (Fraser and Smith, 1974) and the serial pigment pattern of some leptocephali (Smith, 1979) may give the same appearance to potential predators as these elongate rays. All of these structures may be mimicking siphonophores: a remarkable example of convergence (Fig. 10 and 11). Elongate fin spines are heavy and armed with serrations in some. Elongated rays are often precocious in development, with some even forming in the egg. These fin characters seem to vary at the family-species levels. Other characters associated with fin development include the sequence of formation and movement and loss of whole fins or some of the rays. Dorsal and anal fins move forward along the body during larval development in elopiform and clupeiform fishes. They develop in "streamers" in the finfold of argentinoids and attach to the body proper just before or during transformation. The shape of the finfold, presence or absence of a preanal finfold, and shape of the pectoral fin base provide additional characters at the family-genus level.

Gut characters of fish larvae include length and shape as well as the development of a protruding, trailing hindgut in some. In fishes with photophores, their placement and sequence of development are excellent characters at the subfamily-species levels. The eye of a larva is specialized in a number of ways.

→

Fig. 12. Examples of special juvenile stages. (A) *Hexagrammos lagocephalus*, 28.0 mm. A neustonic or epipelagic form of a species that is demersal as an adult (from Kendall and Vinter, 1984); (B) *Forcipiger longirostris*, 17 mm. A spiny form that lives on tropical reefs as an adult (from Kendall and Goldsborough, 1911); (C) *Sebastolobus altivelis*, 26.8 mm. A barred pelagic form of a species that is demersal on the continental slope as an adult (from Moser et al., 1977); (D) *Oncorhynchus kisutch*, 37 mm. The freshwater alevin or parr stage of an andromous salmonid (from Auer, 1982); and (E) *Kali macrodon*, 45 mm. The juvenile of a bathypelagic species. Originally described as *Gargaropteron pterodactylops* (see Johnson and Cohen, 1974).


A
B
C
D
E

Its size and rate of development are useful, as well as whether it is round or oval. Some fish larvae have eyes borne on stalks that reach an extreme in *Idiacanthus,* while others develop an area of choroid tissue. Migration of the eye in flatfish larvae from a symmetrical position to one side of the head is well known. The sequence of development of ossified structures is proving to be a powerful tool in systematic studies of fish larvae. The losses and fusions of bones, which are generally assumed based only on adult material, can and should be tested using developmental studies. The caudal fin skeleton has provided excellent developmental characters to be used for systematic inferences, mainly at the order-generic levels. The development of scales has been little studied but may prove valuable, especially in fishes with precocious scales (e.g., some anthiins, holocentrids).

The Transformation Stage

Between the larval and juvenile stages, there is a transitional stage which may be abrupt or prolonged and which, in many fish, is accompanied by a change from planktonic habits to demersal or schooling pelagic habits (Fig. 12). In some fishes migration to a "nursery" ground occurs during or just before this stage. Morphologically the transformation stage is characterized by a change from larval body form and characters to juvenile-adult body form and characters. At the end of this stage the fish generally looks similar to the adult, with major differences only in pigmentation patterns. Two ontogenetic processes occur during this stage of transition between the larva and juvenile: 1) loss of specialized larval characters, and 2) attainment of juvenile-adult characters. Changes that occur during this stage include pigment pattern, body shape, fin migration (e.g., in clupeids and engraulids), photophore formation, loss of elongate fin rays and head spines (e.g., in epinepheline serranids and holocentrids), eye migration (pleuronectiforms), and scale formation.

In several groups, where the transformation stage is prolonged, the fish have developed specializations that are distinct from both the larvae and juveniles. This stage has been designated the prejuvenile stage (Hubbs, 1943). The specializations generally involve body shape and pigmentation. In many, the morph resembles a herring-like fish and is apparently adapted for neustonic life. The dorsal aspect of the fish is dark green or blue and the lateral and ventral is silvery or white. The body tends to be herring shaped and the mouth terminal. Fins are generally unpigmented. Such a stage is present in Gadiformes (*Urophycis*), Beryciformes (*Holocentrus*), Perciformes (e.g., *Pomatomus,* Mullidae, Mugilidae) and Scorpaeniformes (e.g., *Scorpaenichthys, Hexagrammos*). In other fishes, such as some myctophiforms and carapids, the prolonged transformation stage may have distinctive body and fin shapes.

Implications of Larval Fish Morphology

When studying the appearance of larval fishes, one is immediately struck with their diversity and morphological dissimilarity to adults. This dissimilarity led early workers to establish names for several of these forms, not realizing that they were the young stages of known adults. After establishing the identity of many fish larvae in a variety of groups, we hypothesize that the larvae of all species are recognizably distinct. The use of diversity of larval form in vertebrate systematics was discussed some time ago by Orton (1953b, 1955c, 1957) and in this volume we examine this use in detail in numerous groups of fishes.

Why are the larvae so diverse?—Despite the tremendous mortality associated with living in the planktonic realm during the larval period, survival must be sufficient to maintain the species and provide a dispersal mechanism for it. To different degrees, various taxa apparently rely on survival and longevity of individual larvae. The amount of reliance is presumably related to fecundity and importance of dispersal and colonization to the taxon. A number of structures have evolved that would be expected to enhance larval survival in the plankton. Practically no experimental work has been done to investigate the function of larval structures, but some structures probably assist flotation and feeding while others decrease predator mortality. Convergence on characters that are apparently functionally important to larval survival in the plankton is seen. These specializations develop in conjunction with the basic ontogeny of the taxon. In studying systematics using larval fishes, both the basic pattern of development and the specialized structures must be analyzed.

Why are these larvae so morphologically unlike the adults?—Most larvae are adapted to survive in an ecological realm (generally the plankton) that is far different from that of the adult. These are small organisms, compared to adults, and they live in the plankton, having to find and capture food there and avoid becoming food. They float and migrate vertically in a milieu that may be moving much faster than they are. During this larval period, these fish undergo extreme changes in morphology yet remain a functioning (eating, avoiding predators) organism and eventually end up in a suitable nursery area for the juvenile stage.

How then can larval morphology help us understand the evolution of these fishes?—After recognizing that each species has a morphologically distinctive larva, generally we see that species of the same genus are phenetically similar, and larvae of members of a family also share common features. Even larvae of suborders and orders share some larval characters. This would be expected since evolution operates on all stages in the life cycle, not just the adult. Evolutionary pressures on the larval stage seem to be particularly intense in those groups that rely on the larvae for widespread dispersal in the ocean. Here the larvae appear well adapted for life in the planktonic realm, and it can truly be said that the larva and the adult perform in "two quite separate evolutionary theaters" (Moser and Ahlstrom, 1974). In this volume we are focusing on what we know to date about larval evolution within various groups of fishes (Table 4).

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MATURATION, SPAWNING, AND FECUNDITY OF OPAKAPAKA, *PRISTIPOMOIDES FILAMENTOSUS*, IN THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

The reproductive biology of opakapaka, *Pristipomoides filamentosus*, from the Northwestern Hawaiian Islands was studied. Development of ova within the paired ovaries was heterogeneous, and the stages of maturation, based on the development of ova in the most advanced mode in ova diameter size-frequency distributions, were positively related to the gonadal somatic indices. The data indicated that the spawning season for opakapaka is from June through December, with spawning peaks in August. Fork length appeared to be the best predictor of fecundity. Estimates of annual fecundity ranged from 477,990 ova for a 48.7-cm fish to 1,461,875 ova for a 76.3-cm fish. The species reaches sexual maturity at about 42.5 cm and spawns at 52 cm. The sex ratio (data pooled by years) showed a significant departure from 1:1. More males were observed in January and more females in August. Females predominated in the samples at sizes >70 cm.

fecundity
maturation
sex ratio
Pristipomoides filamentosus
snapper
spawning

INTRODUCTION

In 1978 a tripartite cooperative agreement was signed by the U.S. Fish and Wildlife Service, Hawaii Division of Aquatic Resources, and the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service (NMFS) to investigate the marine and terrestrial resources in the Northwestern Hawaiian Islands (NWHI). Under this agreement, NMFS was responsible for the survey and assessment of benthic and pelagic fishery resources (Uchida et al., 1979).

Part of the Honolulu Laboratory's work included life history studies of commercially important species such as opakapaka, *Pristipomoides filamentosus* (Cuvier and Valenciennes). Opakapaka have been extensively fished around the main Hawaiian islands for decades. Prized for its good taste and pleasing appearance, opakapaka is one of the most important bottomfish in terms of landed weight and cash value.

In this study the spawning season, size at sexual maturity, sex ratio, and fecundity of the opakapaka was examined.

There is a limited amount of data in the literature on the life history and reproductive biology of this deepwater snapper. Ralston (1981) studied the commercially caught opakapaka in the Hawaiian Archipelago and determined that opakapaka was sexually mature at 38-cm fork length (FL) and spawned from July to November.

MATERIALS AND METHODS

For a major portion of the NWHI resource assessment program, the NOAA ship *Townsend Cromwell* was used to survey the bottomfish resource. The opakapaka, as well as other bottomfishes, were caught on handline gear using four hooks (No. 28 size) per line. Samples were collected from most of the banks and reefs from Necker Island to Northampton Seamount at depths of 73 to 220 m.

Landed fish were measured for fork length (FL) and standard length (SL) in millimeters and weighed to the nearest 10 g. Ovaries from 150 fish were collected and preserved in 4 percent buffered formaldehyde-seawater solution. Ovaries were not examined until 6 or more months had passed and shrinkage had stabilized. The developmental stage of all the ovaries was determined by the physical characteristics of the ova (Table 1).

Homogeneity of Ova Development

A pair of ovaries was examined for homogeneity of ova development. A cork borer with an inside diameter of 10.026 mm was used to sample ovarian tissue from the anterior, middle, and posterior regions of both lobes. Each of the core samples extended from the outer layer of the ovary to the central lumen. Each core sample was sectioned into three equal parts, the outer epithelial layer, middle layer, and inner layer adjacent to the lumen, for a total of 18 subsamples. From each of the subsamples, ova were teased from the connective tissue and 200 randomly selected ova was measured. Diameters of the irregularly shaped ova were measured in a petri dish etched with parallel lines. An ocular micrometer was used to measure the ova following the methods of Clark (1934).

TABLE 1. DEVELOPMENTAL STAGES OF THE OVA

Stage	Description	Size Range (mm)
Primordial	Found in all the ovaries; usually ovoid and transparent.	No measurements taken
Early developing	Ova are transparent to translucent; opaque yolklike material may be present in the ovum. Ova usually ovoid or wedgelike.	0.15-0.39
Developing	Ova are completely opaque and ovoid.	0.16-0.67
Advanced developing	Ova are ovoid and have a translucent margin. The fertilization membrane has formed.	0.39-0.60
Early ripe	Ova are usually round or spherical. Yolk material is translucent and oil globules may be present.	0.47-0.58
Ripe	Ova are transparent and contain oil globules.	No ripe ovary collected
Residual	Ova are degenerating and show signs of degradation.	

Source: Adapted from Uchiyama and Shomura, 1974

Fecundity

Estimates of fecundity for five individual fish were obtained by the gravimetric method (Bagenal and Braum, 1968). Preserved ovaries were dried on paper towels and gently squeezed to expel any liquid within the lumen. An electronic balance was used to weigh each pair of ovaries to the nearest 0.1 mg. A middle core sample was extracted from the left lobe and sectioned into three equal layers and each layer was weighed to the nearest 0.1 mg.

Ova were teased from the connective tissues and a random sample of 300 ova were measured to establish the size range of the ova in the most advanced mode. Ova in the most advanced mode were then counted.

Fecundity was estimated from each subsample by multiplying the number of ova in the most advanced mode by the ratio of the total ovary weight divided by the subsample weight. The mean of these estimates was used to represent the fecundity of the fish.

Relationships of fecundity to fish length and body weight were examined by plotting fecundity estimates against lengths and weights. Regression lines of the form $Y = a + bX$ (where Y = log of the number of ova, X = fish length in centimeters or weight in kilograms) were fitted by the least squares method.

RESULTS

Homogeneity of Development

Because the frequency distributions of the ova diameters (see Table 1) from the 18 subsamples were skewed to the right of the means, a Kruskal-Wallis, nonparametric test (Sokal and Rohlf, 1969) was used to compare the 18 subsamples. The results showed that the variances among the sites were significantly different ($\chi^2 = 191.45$, d.f. = 17, $P < 0.01$), indicating that the ova in opakapaka ovaries developed heterogeneously.

Fecundity

Fecundity estimates ranged from 478,000 for a 48.7 cm fish to 1,462,000 for a 76.3 cm fish. Relationships of the log fecundity to fork length and weight were determined by the least squares method. The relationship between fecundity and fork length gave the best fit ($r^2 = 0.90$) (Figure 1). The relationships of fecundity to length and weight were:

$$\begin{aligned} \log \text{fecundity} &= 4.74 + 0.0187\ FL \\ r^2 &= 0.90 \text{ and} \\ \log \text{fecundity} &= 5.43 + 0.108\ wt \\ r^2 &= 0.87 \end{aligned} \tag{1}$$

where FL is in centimeters and wt in kilograms.

Spawning Seasonality

The gonadal somatic index (GSI) can be used to estimate the spawning season, provided that it can be shown to have a positive relationship with the various stages of ovarian maturity. A test to determine the relationship between fish size and GSI indicated that fish size was positively correlated with GSI ($r = 0.447$, d.f. = 137, $P < 0.01$). A test between fish size and stages of maturity also showed positive correlation ($r = 0.873$, d.f. = 131, $P < 0.01$) (Figure 2). It appeared that as the female developed sexually, the weight of the ovary not only increased faster than that of the total body weight, but also rose and fell in relation to ovary development, spawning, and redevelopment.

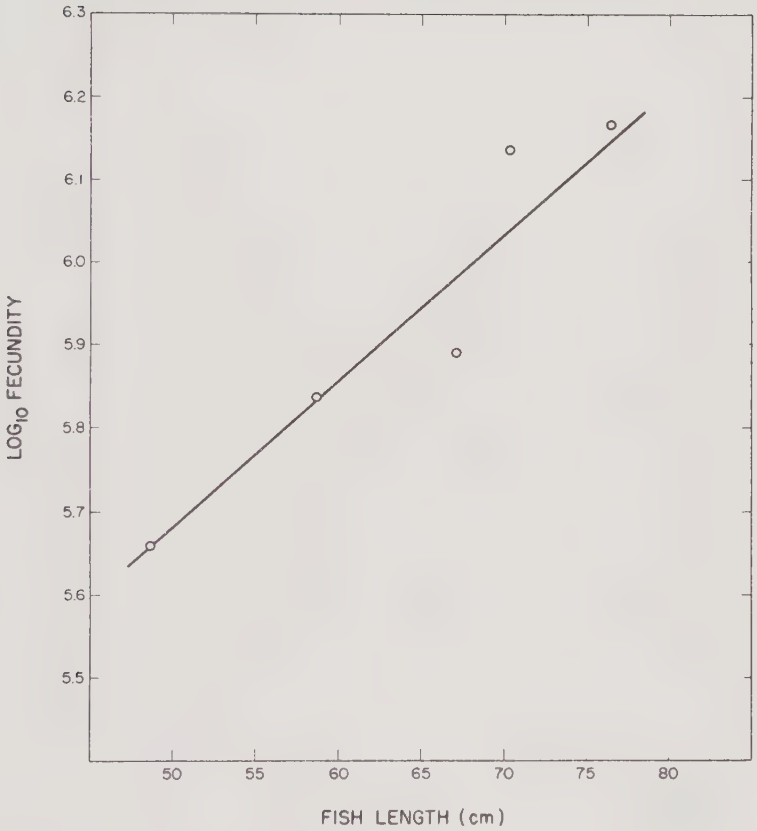

Figure 1. Relationship between the log of fecundity and the fish length (fork length) of opakapaka from the Northwestern Hawaiian Islands

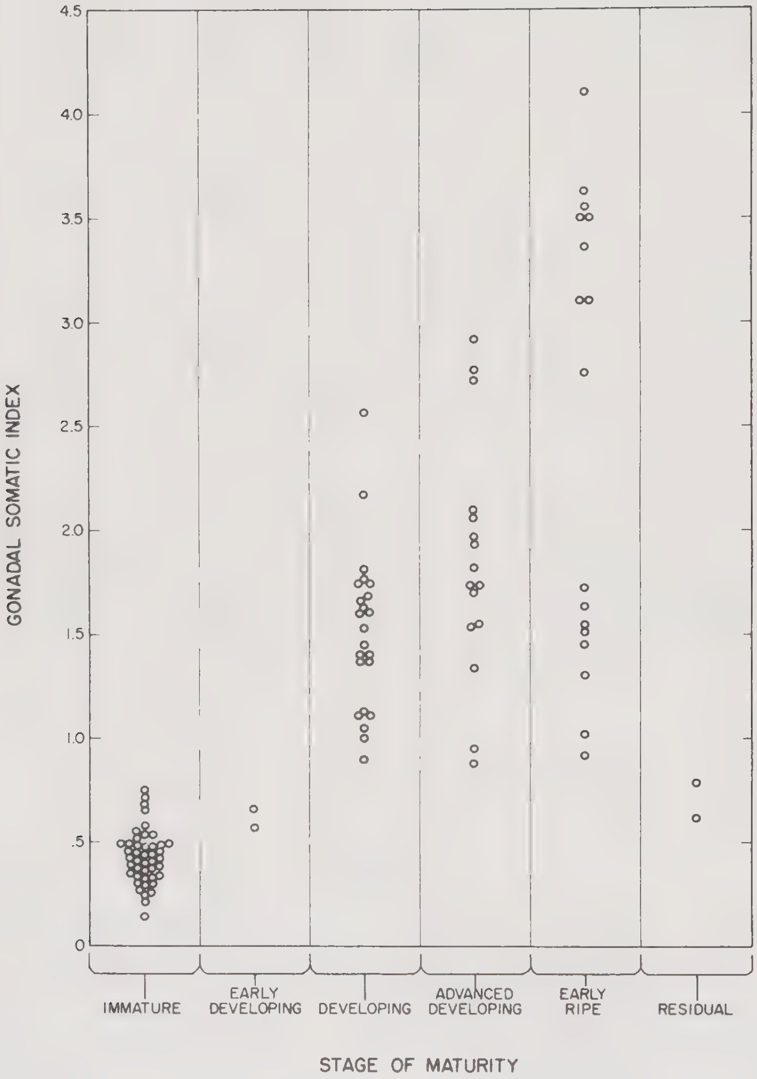

Figure 2. Relationship between stages of maturity and gonadal somatic index in the opakapaka

The spawning cycle of the opakapaka was determined by plotting the GSI against the month of capture (Figure 3). The results showed that spawning commenced in June (GSI = 3.5 percent) and peaked in August (GSI = 4.1 percent). At the conclusion of the spawning season in December, the GSI was 3.1 percent. The lowest GSI was found in January. However, the occurrence of ripening ovaries during this period suggests a protracted spawning season.

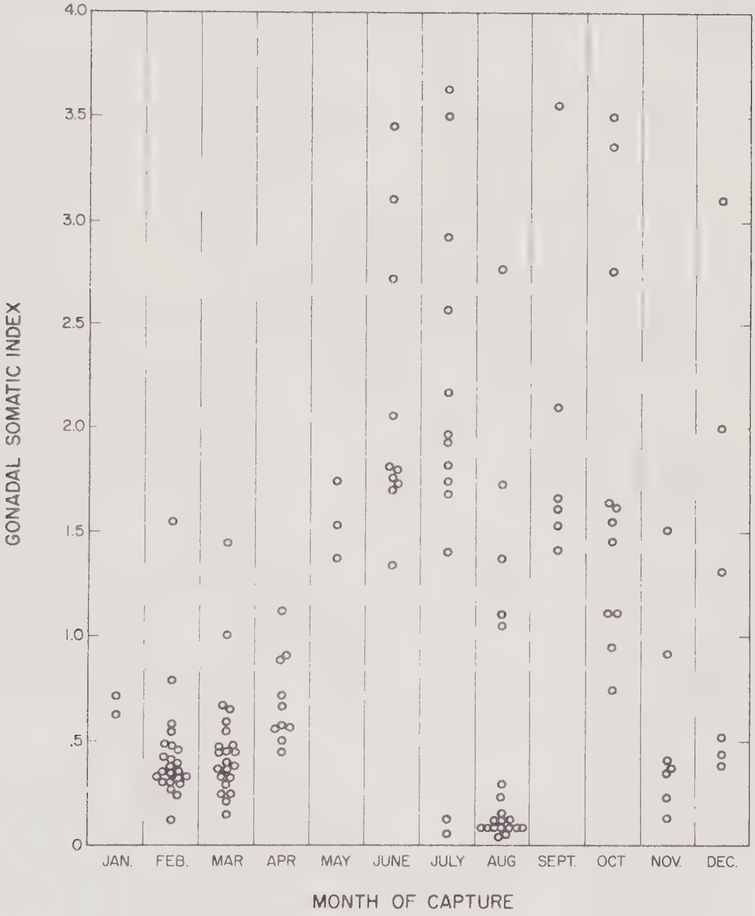

Figure 3. Gonadal somatic index of 135 female opakapaka by month of capture

Size of Maturity

Since it was determined that fish size was closely related to sexual development, size at maturity of the opakapaka was determined by the percentage of change in mean gonad weight at each 5-cm size class (Figure 4). The greatest percentage of increase in gonad weight is expected when a fish matures. For the opakapaka the greatest percentage of increase in gonad weight was observed at the 40 to 50-cm class. The data indicate that opakapaka mature at about 42.5 cm. The smallest mature fish was 42.7 cm. The smallest ripe fish was 37.4 cm and was probably a precocious fish.

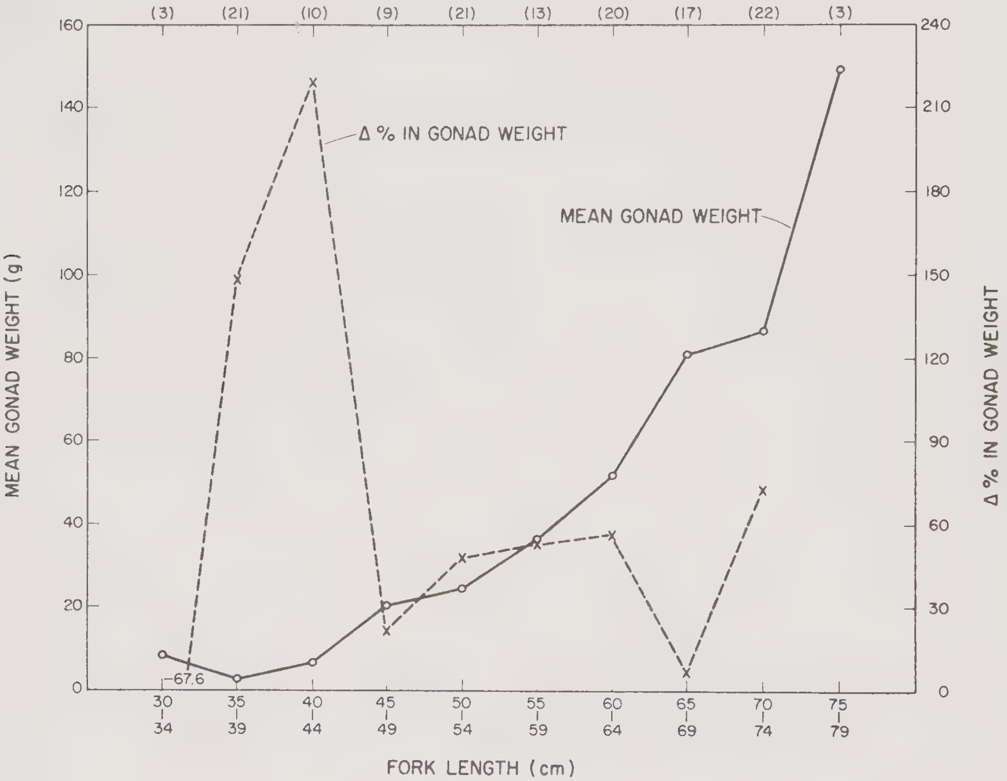

Figure 4. Ovary weight and percent change in ovary weight by 5-cm size classes (sample size in parentheses)

Sex Ratio

Sex data were obtained for 643 opakapaka during the 4 years of the resource assessment program. Because the yearly sex ratios did not deviate significantly from the expected (Table 2), the data for 1978, 1979, 1980, and 1981 were pooled. Females

TABLE 2. NUMBER OF MALE AND FEMALE OPAKAPAKA COLLECTED BY MONTH AND YEARS, 1978 THROUGH 1981

Month	Year				Total	d.f.	χ^2
	1978	1979	1980	1981			
January	61:35	—	—	2:3	63:38	1	6.19*
February	3:8	—	—	11:19	14:27	1	4.12*
March	14:34	—	11:8	0:1	25:43	2	4.76*
April	—	10:9	4:10	4:0	18:19	2	0.03
May	3:5	0:1	—	6:11	9:17	2	2.46
June	12:10	—	9:17	5:11	26:38	2	2.25
July	—	3:5	—	22:21	25:26	1	0.02
August	10:18	—	4:16	9:22	23:56	2	13.78†
September	4:1	1:2	18:12	—	23:15	2	2.19
October	38:34	—	11:5	—	49:39	1	1.14
November	2:3	—	12:12	—	14:15	1	0.03
December	—	4:3	2:6	—	6:9	1	0.60
TOTAL	147:148	18:20	71:86	59:88	295:342		
d.f.	1	1	1	1			
χ^2	0.003	0.11	1.43	5.72*			

Note: The deviation of the male to female ratio from an expected 1:1 was tested by Chi-square.

*$P \leq 0.05$
†$P < 0.01$

were more abundant than males. For the pooled sample, the male to female ratio of 1:1.18 significantly differed from the expected 1:1 ($\chi^2 = 4.37$; d.f. = 1; P = 0.05).

Monthly sex ratios deviated significantly from 1:1 on four occasions. Larger numbers of males were caught in January and by contrast females were more numerous in February. Also during the peak spawning period in August, females were more predominant than males by 2.43 times.

When size of the fish was considered, the sex ratio deviated from the expected in two size groups. Females were more numerous in the 30 to 39-cm class (1.92:1) and in the largest size class, 70 to 79 cm (1.96:1) (Table 3).

TABLE 3. NUMBER OF MALE AND FEMALE OPAKAPAKA GROUPED IN 10-CM SIZE CATEGORIES

Fork Length (cm)	Males	Females	n	χ^2
20-29	1	5	6	2.67
30-39	36	69	108	10.37*
40-49	59	66	125	0.39
50-59	86	74	160	0.90
60-69	88	83	171	0.15
70-79	25	49	74	7.78*

Note: Deviation of the sex ratio from the expected 1:1 was tested by Chi-square.

*P < 0.01

DISCUSSION

The distribution of ova in various stages of development throughout the 18 subsamples indicated that development of the ovary in the opakapaka was heterogeneous. Of the total 18 subsamples from 1 fish, only 6 subsamples had ova in the advanced developing stage and only 2 subsamples had ova in the ripe stage. In the test for homogeneity of location, developing ova were used because of their consistency throughout the 18 subsamples.

It appears likely that opakapaka spawn more than once in the protracted spawning period of 7 months. During the spawning season, only 2 percent of the females of mature size had indices lower than 1 percent which occurred only at the conclusion of the period. Also, all of the sexually mature females during that time exhibited either developing or ripening ovaries and none was found in a spent or resting condition. From the continuous development of the intraovarian ova and the absence of resting ovaries during the spawning period, it is concluded that the opakapaka is probably an intermittent spawner.

Spawning is probably initiated by transient environmental conditions that promote rapid ova development and optimize development and survival of the short planktonic life of the lutjanid larvae (Randall and Brock, 1960).

Occurrence of ripe ovaries substantiated the spawning period indicated by the seasonal distribution of GSI. More sexually developed fish were observed in October: 46 percent of the fish had ripening ovaries. Ralston's 1981 work on commercially caught opakapaka indicated that the fish spawns from July through November.

Although the yearly sex ratios for 1978-81 did not deviate significantly from the expected, the sex ratio for the pooled sample deviated significantly from 1:1 in favor of the females. Kami (1973) observed significantly higher catches of male opakapaka in Guam, whereas Ralston (1981) found no predominance of any sex in his study of P. filamentosus caught in Hawaii.

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GONADAL MATURATION, FECUNDITY, AND SPAWNING OF THE GREATER AMBERJACK, *SERIOLA DUMERILI* (RISSO), IN HAWAIIAN WATERS WITH REFERENCES TO CIGUATOXIN INCIDENCES

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ABSTRACT

Reproductive biology of the greater amberjack, *Seriola dumerili*, was investigated to determine relationships with the irregular occurrence of ciguatoxic fish in Hawaiian waters. Incidence of toxic fish was independent of ovary maturity and spawning season. The spawning season is from February through June and peaks in March and April. Incidental spawning occurs year-round. Amberjack appears to be an intermittent spawner with three to four major spawnings in the relatively long protracted spawning season. Size at first maturity was 72-cm fork length and ripe ovaries were first observed in fish 78 cm long. Estimates of fecundity ranged from 1.3 to 4.2 x 10^6 ova for the 83.0 to 118.6-cm size group. Sex ratio was 1.09:1 (males to females); males predominated among fish 60 to 79 cm in length and females among fish 100 cm in length.

ciguatera
fecundity
reproduction
Seriola dumerili
spawning season
greater amberjack

INTRODUCTION

Until May 1980, the greater amberjack, *Seriola dumerili*, comprised a substantial amount of the handline fishery landings in Hawaii, ranking third with an annual average catch of about 33,107 kg (DAR, 1980). Irregular occurrences of ciguatera poisoning (Halstead, 1970) which implicated the amberjack have virtually eliminated commercial sales.

In April 1979, a 2-year program was initiated by the Honolulu Laboratory, Southwest Fisheries Center, National Marine Fisheries Service (NMFS), with the University of Hawaii School of Medicine, and the United Fishing Agency (UFA) to develop a practical method to screen commercial fishes for ciguatera. Due to its history of implication in ciguatera poisoning, the amberjack was employed as a test species.

Previous workers (Hiyama, 1950; Watanabe, 1950; Cooper, 1964) have hypothesized that ciguatera poisoning is directly related to maturity and gonadal ripeness of the fish. A preponderance of toxic fish might occur during the spawning seasons. Banner et al. (1966) have found that elimination of the ciguatoxin in _Lutjanus_ _bohar_ was very slow such that after 30 months there was no detectable drop in toxicity level. They inferred that the incidence of toxicity would be higher in the larger, mature fish.

Of the few studies conducted on the reproductive biology of the greater amberjack, none has examined its relationship with ciguatera levels. Burch (1979) observed that peak spawning in the western Atlantic occurred in March through June with evidence of year-round incidental spawning. Similar fecundity and maturation studies of _S_. _dorsalis_ off California have demonstrated that multiple spawning occurs from July to October (Baxter, 1960).

In this study, some aspects of reproduction of an exploited fish stock including (1) spawning season, (2) fecundity, (3) size at first maturity, and (4) sex ratio have been determined and compared with the occurrence of ciguatoxin.

MATERIALS AND METHODS

A total of 5,242 amberjack gonads were collected from April 1979 through April 1981 for ciguatera screening. Fish sampled were caught by commercial handline boats in the area between the island of Hawaii and Pearl and Hermes Atoll in the Northwestern Hawaiian Islands.

Fork length (FL), body weight (to the nearest 0.1 kg), date, and location of capture, when available, were recorded. Gonads and stomachs were removed and frozen for laboratory examination. Tissue samples extracted from various parts of the body were collected for ciguatoxin analysis using a radioimmunoassay technique developed by Hokama et al. (1977) at the John A. Burns School of Medicine, University of Hawaii.

Frozen gonads were weighed to the nearest gram and larger more developed ovaries were preserved in modified Gilson's fluid (Simpson, 1951) for fecundity estimates. Other ovaries were preserved in 4 percent formaldehyde solution. Testes were weighed and discarded.

To facilitate the penetrations of the Gilson's fluid, epithelium of the ovary was slit longitudinally on both lobes and inverted, exposing the sinuous germinal tissues. Daily agitations of samples over a 3 to 6-week period enhanced the digestion deterioration of the connective tissues and freeing of the hardened ova. Remaining connective tissue was sufficiently broken down so that any attached ova could be easily freed. Ova were separated from remaining tissue with a 1-mm mesh nylon screen, then collected and washed over a 0.183-mm mesh screen.

Subsamples for fecundity estimates were obtained by a volumetric method (Van Dalsen, 1977) with minor modifications. In place of a reversing magnetic stirrer, ova were initially suspended with a stirring rod. Then, an unidirectional magnetic stirrer was activated to create a counterflow. Prior to the formation of a vortex, two 5-ml aliquots were drawn with a pipette from the lower two-thirds of the mixture, and approximately 2 to 5 cm from the wall of the container.

Estimates of fecundity (F) were obtained by the following formula:

$$F = \frac{\sum^{n} N}{n} \bullet \frac{V}{5 \text{ ml}}$$

where

n = number of subsamples
N = number of ova in each subsample
V = total volume of the mixture in milliliters

Eight ovaries were sampled during the 1980 spawning season for fecundity estimates. Relationships of fecundity with FL, body weight (wt), and gonad weight (gw) were compared using Bartlett's "three-group" method for model II regression (Sokal and Rohlf, 1969; Ricker, 1973). Also from each of the subsamples, 300 randomly selected ova were measured and staged under a microscope (Kikkawa, 1980). Due to the irregular shape of the preserved ova, diameters were measured following the method of Clark (1934).

Earlier workers have customarily used ova diameter frequency distribution in spawning studies (Clark, 1934; Yuen, 1955; Otsu and Uchida, 1959). Although this method provides a good estimate of maturity, the technique is quite laborious. Due to the large number of samples, a simpler method was desirable. Bagenal and Braum (1968) suggested the use of gonad weight as an indicator of reproductive condition. Consequently a percent ratio of gonad weight to body weight (gw/wt x 100), termed the gonadosomatic index (GSI), was employed to represent maturity. For comparative purposes, the developmental stage of ovaries was also determined on the basis of the most advanced ova in the ovaries.

RESULTS

Developmental Stages of the Ovary

Seven stages of ova development could be identified based on physical characteristics: immature, early developing, developing, advanced developing, early ripe, ripe, and residual (Table 1). These stages were similar to those found by Uchiyama and Shomura (1974) in the swordfish, *Xiphias gladius*, and Kikkawa (1980) in the pink snapper, *Pristipomoides filamentosus*.

Ova diameter distributions of ova in various stages of maturity are shown in Figure 1. Primary or primordial cells occurred in all of the ovaries. These rudimentary cells were not measured.

Early developing ova made up the "developing" mode. They were considered unlikely to be released during the next spawning. The "ripening" category included ova in a wide developmental stage from "developing" to "early ripe" (Table 1). No running ripe ova were observed.

The developmental stage assigned to an ovary was based on the most advanced ova. Immature and recently spent females with only primordial cells in the ovaries were considered to have nondeveloping ovaries. Those with ova in the "developing" mode (Figure 1) were classified as developing. Ovaries were classified as "ripening" based on the presence of ova in "advanced developing" mode which included ova in the developing to ripe stage.

TABLE 1. DESCRIPTION OF THE OVARIES OF GREATER AMBERJACK AT VARIOUS STAGES OF DEVELOPMENT

Ova Maturity Stage		GSI Mean (±S.E.)	Physical Description of the Oocytes	Diameter μm x 10^2	Ovary Maturity
I.	Primordial	0.940 (0.059)	Oocytes prevalent in all ovaries; oocytes are usually ovoid and consist of uniform transparent gelatinous material.	--	Nondeveloping
II.	Early	0.701 (0.052)	Oocytes are semitransparent to translucent due to the formation of granular yolk matter. Oocytes are usually ovoid or wedgelike.	2.0-5.1	Developing
III.	Developing	0.701 (0.279)	Oocytes are completely opaque with yolk material.	4.1-6.9	Ripening
IV.	Advanced developing	2.80 (0.099)	Oocytes are usually spherical with uniform opaque yolk granules and encased in a transparent fertilization membrane.	4.6-7.4	Ripening
V.	Early ripe	3.78 (0.55)	Oocytes are usually spherical. The yolk material is translucent; oil globules are present.	5.1-7.6	Ripening
VI.	Ripe	4.86 (0.16)	Oocytes are usually almost transparent; oil globules are present.	--	Ripening
VII.	Residual	3.80	Oocytes show signs of reabsorption. Cells are translucent and greatly reduced.	4.8-7.0	Ripening

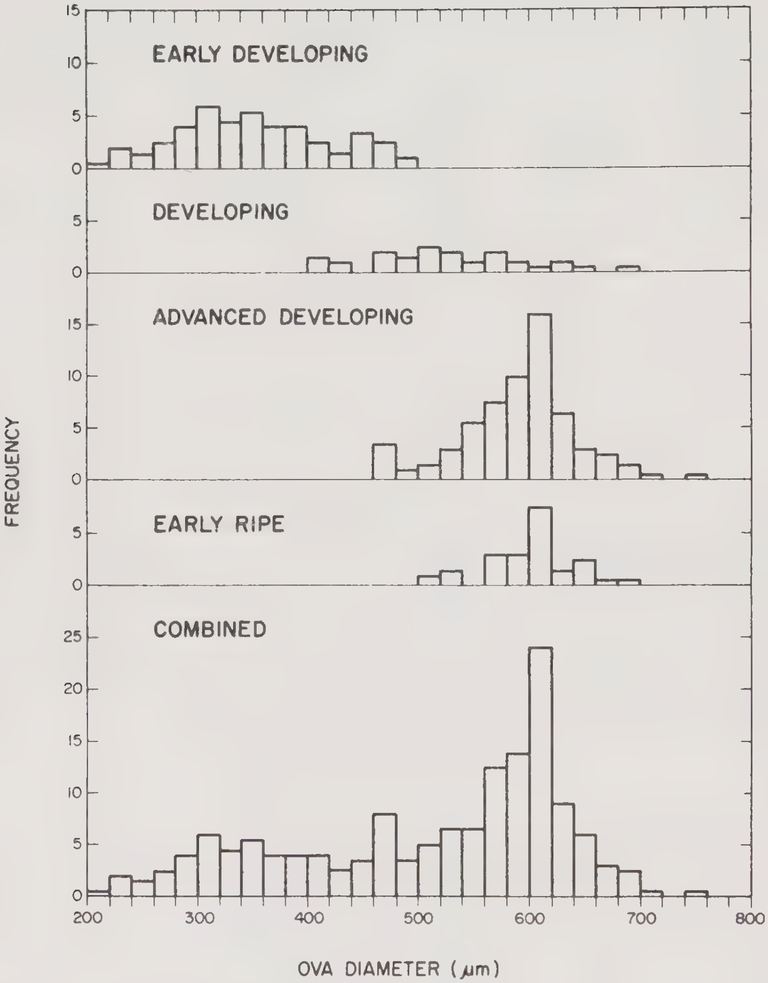

Figure 1. Size-frequency distribution of ova at various stages of maturation

Fecundity

In eight ripening females (83.0 to 118.6-cm FL), fecundity ranged from 1.3 to 4.2 x 10^6 ova. The relationships of fecundity to length, body weight, and gonad weight were linear. Bartlett's method for model II regression was used to describe the relationship:

Relationships	d.f.	Results
Fecundity and length	7	$F = -0.71 + 0.0025\ FL$ $r^* = 0.72$
Fecundity and body weight	7	$F = 0.97 + 0.05\ wt$ $r^* = 0.82$
Fecundity and gonad weight	7	$F = -0.24 + 0.0036\ gw$ $r^* = 0.89$

where

F = fecundity x 10^6
FL = fork length in centimeters
wt = body weight in kilograms
gw = gonad weight in grams
r^* = the unbiased correlation coefficient (Kendall and Stuart, 1967)

All developing and ripening ova in the most advanced mode were used to estimate fecundity. The fecundity was best correlated with gonad weight. Gonad weight, therefore, was considered the best predictor of fecundity.

Ovary maturity and gonadosomatic index

Females that (1) were too small to be sexually mature, (2) had ovaries containing only primordial cells, (3) had ovaries containing early developing oocytes, and (4) were recently spent had indices of about 1 percent. Females with indices 2.0 percent were considered to be sexually active and expected to spawn in the current spawning season. Fish with near ripe ovaries had indices 3.5 percent. The highest index for a female was 4.86 percent.

Spawning season

The seasonal distribution of GSI indicated that spawning began in February, peaked in March and April, and concluded by July (Figure 2). Mean GSI reached 2.5 percent for males and 3.0 percent for females in February and rose to 5 percent for males and 4.5 percent for females in March. At the conclusion of the spawning period, GSI declined to about 1.8 percent for both sexes. The occurrence of a few ripe ovaries and low mean GSI levels throughout the year indicates that incidental year-round spawning may occur.

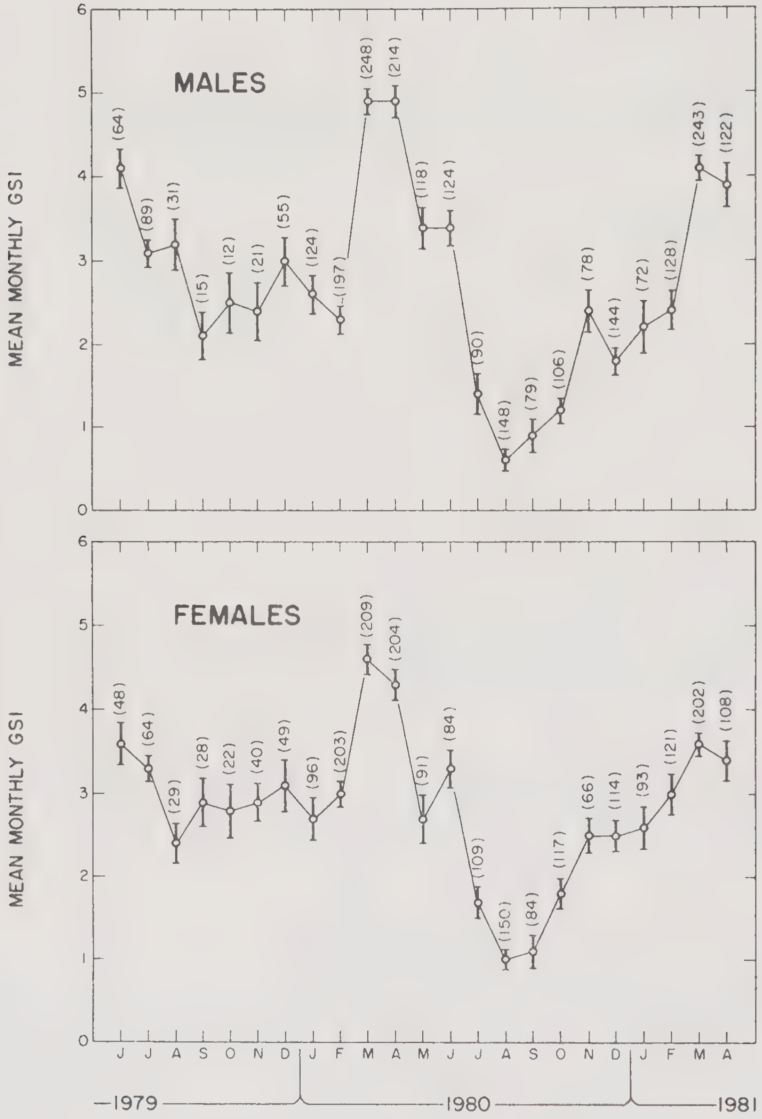

Figure 2. Mean monthly gonadosomatic index (GSI) for the greater amberjack. The vertical lines represent ± standard error of the mean; (N) is sample size.

Size at maturity

The relationship between body length and the development of ovaries was determined from 144 randomly selected ovaries. The percentage of females with nondeveloping, developing, and ripening ovaries was plotted by 2-cm size classes to determine size at maturity. Females with developing ovaries were considered mature and those with nondeveloping ovaries, immature. At 70 cm every female was immature; however, at 72 cm 40 percent had reached maturity. Thus, females were considered likely to reach maturity at 72 cm (Figure 3). The smallest female with ripe ovaries measured 78 cm and was estimated to be 2.5 years old (J.H. Uchiyama, 1983: personal communication).

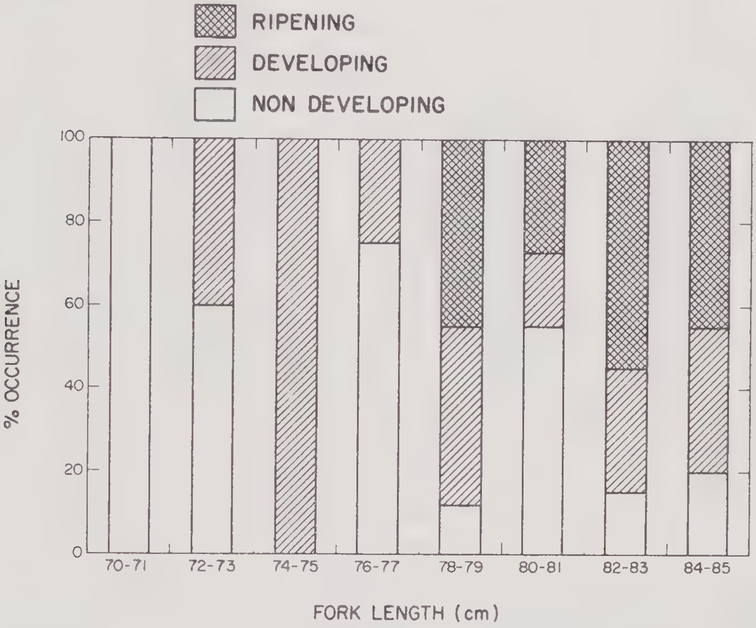

Figure 3. Percentage of distribution of ovaries in various stages of development by fish size

Sex ratio

Males predominated (1.09:1) in the 5,242 fish sampled for this study. Sex ratios by year were: 1979, 1.01:1; 1980, 1.11:1; and 1981, 1.10:1. The sex ratio for 1980 deviated most from the expected 1:1 ratio. Pooled by year, the sex ratio deviated significantly from 1:1 in March, June, and December (Table 2). For the 10-cm length classes, sex ratio deviated from 1:1 for most of the size categories (Table 3). Generally the males predominated in the larger sizes (≤100 cm). Among the smaller sizes (≤60 cm), no significant deviations from the expected were found.

TABLE 2. DEVIATION OF THE MALE TO FEMALE SEX RATIO FROM 1:1 IN GREATER AMBERJACK BY MONTH AND YEAR

Month	Year			Total a	d.f.	χ^2
	1979	1980	1981			
April	29:16	221:221	122:112	372:339	2	1.53
May	43:69	121:94	--	164:163	1	0.003
June	101:72	137:93*	--	238:165	1	13.22†
July	89:64	92:111	--	181:175	1	0.10
August	31:29	150:151	--	181:180	1	0.003
September	15:28	83:87	--	98:115	1	1.36
October	14:26	108:119*	--	122:145	1	1.98
November	23:41	81:69	--	104:110	1	0.17
December	55:50	159:122	--	214:172	1	4.57
January	--	128:97	73:93	201:190	1	0.31
February	--	202:203	129:123	331:326	1	0.04
March	--	265:216	267:208	532:424	1	12.20*
Total b	400:395	1,747:1,583	591:536			
d.f.	8	11	3			
χ^2	0.03	8.08	2.68			

Note: Total a = the sex ratio pooled by month for all years; Total b = the sex ratio for each year

*$P < 0.05$
†$P < 0.01$

Incidence of ciguatoxic fish

Of the 5,227 amberjacks tested, 370 males and 372 females had high levels of ciguatoxin. The percentage of toxic males (13.6 percent) from that of females (14.9 percent) was not significantly different ($t = 1.6934$; d.f. = 5,226; $P > 0.05$).

TABLE 3. DEVIATION OF THE MALE TO FEMALE SEX RATIO FROM 1.09:1 IN GREATER AMBERJACK BY 100-MM SIZE CATEGORIES

Fork Length (mm)	Male	Female	n	χ^2
400	27 (39.7)	41 (60.3)	68	2.88
400-499	104 (46.0)	122 (54.0)	226	1.43
500-599	202 (52.3)	184 (47.7)	386	0.84
600-699	393 (57.4)	292 (42.6)	685	14.89*
700-799	835 (58.1)	601 (41.9)	1,436	38.13*
800-899	815 (54.1)	692 (45.9)	1,507	10.04*
900-999	282 (46.3)	327 (53.7)	609	3.33
1,000-1,099	40 (24.1)	126 (75.9)	166	44.55*
1,100-1,199	7 (13.0)	47 (87.0)	54	29.63*
1,200-1,299	1 (4.4)	22 (95.6)	23	19.17*
1,300	0 (0)	6 (100)	6	--

Note: percentages given in parentheses

*$P < 0.01$

A 2 x 3 contingency table of nontoxic and toxic females against stages of ovary development was constructed to show variations in the occurrence of toxic females by maturity (χ^2 = 9.517; d.f. = 2; $P < 0.01$). A test of independence showed that toxic female amberjacks were most likely to have immature or ripening ovaries (χ^2 = 9.668; d.f. = 2; $P < 0.01$) (Table 4).

TABLE 4. PERCENT DISTRIBUTION OF TOXIC AND NONTOXIC FISH AT VARIOUS DEVELOPMENTAL STAGES

Developmental Stage	Nontoxic	Toxic
Developing	86.0 (3,353)	14.0 (544)
Developing	84.8 (890)	15.2 (159)
Ripe	84.4 (464)	15.6 (86)
TOTAL	100.00 (4,707)	100.00 (789)

Note: Sample size is given in parentheses

No obvious trends in the relationship between the seasonal distribution of toxic fish and spawning could be detected. During 1980, occurrence of ciguatoxic fish peaked in January, March, June, August, and October. The mean percentage was 22 percent of the total month's catch.

DISCUSSION

In this study, fecundity is defined as the number of eggs in the female likely to be extruded at the next spawning (Bagenal and Braum, 1968). Ova in this category were those in the most advanced mode in the ova diameter frequency distribution. It was unlikely that the ova in the secondary mode would develop enough to be released with ova in the most advanced mode. Although the developmental rate of the ova was not determined and the advanced mode included ova in various developmental stages from developing to early ripe, it was assumed that at the time of spawning all of the ova in the most advanced mode would be extruded. Work on the jack mackerel off California demonstrated the occurrence of two major spawnings, i.e., the two modal groups of ova suggested a spawning with each mode.

The seasonal distribution of GSI did not indicate a second peak spawning during the relatively long breeding season, which was estimated to last from February to June, but the possibility of multiple spawning cannot be ignored. It is apparent from the multimodal distribution of ova diameters that the ova in the secondary mode would unlikely develop enough in size and maturity to be released with ova in the most advanced mode. Based on the continuous development of ova, it seems likely that the greater amberjack is a multiple spawner. Although there are no data to determine the number of spawnings per season, higher occurrences of juveniles (fish <45 cm and with sexually indistinguishable undeveloped gonads) in May, July, September, and October (Figure 4) could possibly reflect three or four major spawnings in the spring.

During the off-spawning season, the infrequent catches of ripe fish and a few juveniles indicate that incidental spawning may occur. Spawning would be closely associated with environmental conditions conducive to larval fish survival as was demonstrated for the Japanese horsemackerel, *Trachurus japonicus* (Chigirinskiy, 1970).

The spawning season for greater amberjack off the coast of Florida is from March to June, peaking in April and May. It was inferred from the infrequent catches of ripe fish that the amberjack exhibit low year-round spawning (Burch, 1979). Also, larval fish surveys in the eastern Gulf of Mexico and Straits of Florida tend to support the generalization that year-round spawning is typical of the *Seriola* spp. (Dooley, 1972; Munro et al., 1973; Aprieto, 1974; Fahay, 1975).

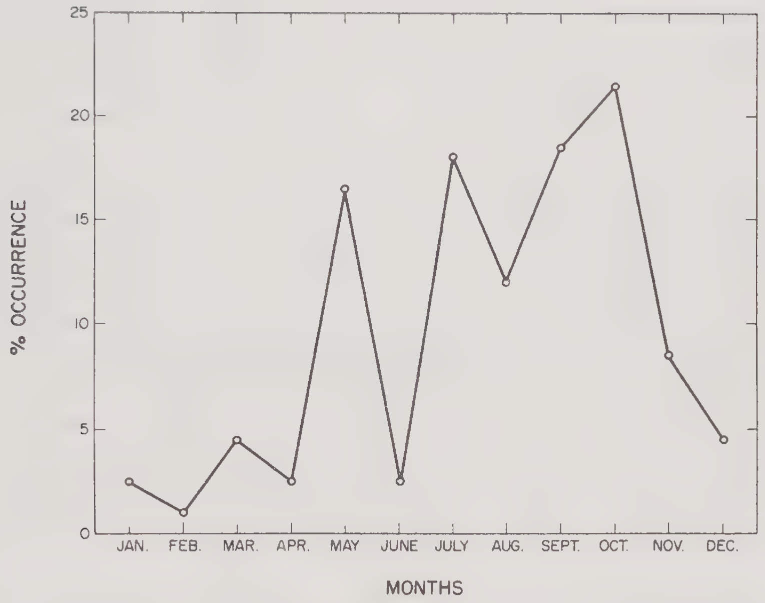

Figure 4. Percentage of distribution of juvenile amberjack ≤ 45 cm throughout the year

The literature on sex ratio provided little assistance in interpreting the significant variations from a 1:1 sex ratio. Deviations from the expected ratio could be due to sexual differences in longevity, growth, mortality, and behavioral patterns, or to sex reversal and migration of one sex out of the sampling area as suggested by Wenner (1972). Of these, only differences in mortality and longevity are supported by available evidence. The number of males in the midsize classes (60 to 90 cm) were significantly greater than the females. Conversely, fish ≥ 100 cm were predominantly females.

The occurrence of 12.2 percent immature and 16.9 percent ripening toxic fish is contradictory to the hypothesis that toxicity is related to spawning period and gonad development (Hiyama, 1950; Watanabe, 1950). No significantly higher number of toxic ripening fish was found. Investigators studying the acquisition and retention of ciguatoxin in the red snapper, Lutjanus bohar, have found that toxicity levels remained the same for about 30 months and that elimination of the toxin is very slow (Banner et al., 1966). Due to the persistence of the toxin, one would expect a higher percentage of toxic fish to have reached sexual maturity, but we did not find this to be so. A possible explanation of this anomaly is that at various stages of development, ciguatoxin could be concentrated in different organs. Higher levels of the fat soluble toxin (Scheuer et al., 1967) might be in tissues of high lipid concentrations such as the generative tissues at the onset of spawning. Substantiating work on sardines, herring, and other cluepids have elucidated the increase of fats in the musculature, mesentery, and viscera preceding the onset of spawning (Blaxter and Holliday, 1963; Channon and El Saby, 1932). At the onset of spawning, fat reserves are channeled to the gonads as energy source and nutritive materials in the yolk (Shul'man, 1974). A close association of ciguatoxin with the homologous lipids (Lasker and Theilacker, 1962) might be expected and like the lipids, toxin might be concentrated in different organs due to physiological changes in the fish. During the prespawning period, movement of fat reserves to the reproductive organs would create a lipid and ciguatoxin gradient, thereby increasing the toxicity level in the viscera. Some ciguatera attacks were thought to be caused by the consumption of the more toxic viscera than the musculature (Halstead and Schall, 1958; Cooper, 1964; Helfrich et al., 1968). In immature or resting fish, higher concentrations of toxin would likely be in the musculature due to the rising fat reserves. Because only the musculature was tested by radioimmunoassay, this question remains unresolved.

SUMMARY

1. Greater amberjack gonad samples were collected from the Hawaiian commercial fishery from April 1979 through April 1981 as part of a ciguatera research program.

2. Fecundity estimates, based on counts of all ova in the most advanced mode, ranged from 1.32×10^6 to 4.2×10^6 for fish from 83.0 to 118.6 cm. Relationships of ova count to gonad weight, body weight, and length were best decribed by model II regressions. Gonad weight was the best predictor o fecundity.

3. Spawning season for the amberjack was February through July, peaking in March and April.

4. Infrequent occurrence of ripe ovaries and low mean GSI levels throughout the year indicated year-round incidental spawning.

5. Based on the occurrence of juveniles <45 cm and continuous ripening of the ova during the relatively long spawning period, it appears that the amberjack are intermittent spawners; it is possible that there may be three to four major spawnings in a single season.

6. Size at maturity was estimated to be 72 cm. Some fully ripe individuals were 78 cm.

7. The male to female sex ratio of the 5,242 amberjack sampled was 1.09:1, differing significantly from the expected 1:1 ratio. Males predominated among the midsizes (60 to 79 cm) whereas, females predominated in the larger sizes (≥ 100 cm).

8. The incidence of ciguatoxic fish was neither related to spawning season nor to sex.

9. There was a slightly higher rate of toxic females in the immature and ripening stages.

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THE SEXUALITY OF TROPICAL DEEPWATER SHRIMPS (DECAPODA: PANDALIDAE)

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ABSTRACT

Morphometric studies were carried out as part of resource assessment surveys on deepwater pandalid shrimps in both the northern and southern tropical Pacific Ocean.

Previous works have suggested that pandalid shrimps, including those of some tropical species, are typically protandrous hermaphrodites. In this study, however, measurements of certain male secondary sexual characteristics were positively correlated with shrimp size. There was no evidence of degeneration of these characteristics in larger individuals as would be expected with protandrous hermaphrodites. We conclude that shrimps of the tropical pandalid species examined are dioecious and that sex reversal does not occur.

Sex reversal in pandalid shrimps was first noted in *Pandalus danae* (Berkeley, 1929) and, since that time, has been reported for a large number of exploited pandalids from northern temperate waters including *P. jordani* and *P. borealis* (Butler, 1964). Butler stated that, with "one or two known exceptions," all pandalid shrimps so far investigated were protandrous hermaphrodites.

The usual pattern in hermaphroditic pandalid shrimps is for individuals to mature and function first as males and, at two or three years of age, to change sex and function as females. During the change in sex, the appendices masculinae on the endopods of the second pair of pleopods of the male degenerate during a series of intersex or transitional stages, until these structures are entirely lacking in females.

Deepwater pandalid shrimps are also widely distributed in the tropical Pacific Ocean, including Hawaii (Clarke, 1972; Struhsaker and Aasted, 1974), Guam (Wilder, 1977), New Caledonia (Intès, 1978), Fiji (King, in press), Tahiti (Anonymous, 1979), Western Samoa (King, 1980), Vanuatu, west of Fiji (King, 1981a), Tonga (King, 1981b), Papua New Guinea (King, 1982), and the Northern Marianas (Moffitt, 1983). Some species, particularly of the genus *Heterocarpus*, are found in sufficient abundance to stimulate interest in commercial exploitation (King, 1981c). Shrimps of several of these species including *H. ensifer* (Clarke, 1972), *H. ensifer* and *H. laevigatus* (Wilder, 1977), and *H. sibogae* and *H. laevigatus* (King, 1981a) were thought to be protandrous hermaphrodites similar to temperate pandalid species.

During studies on the biology and commercial potential of deepwater shrimps in Fiji and the Marianas, at least thirteen different species have been found (Table 1). This paper examines the morphometry and the sexuality of five species which were obtained in sufficient numbers and over a wide size range. The species examined were *Plesionika longirostris, H. ensifer, H. sibogae, H. gibbosus,* and *H. laevigatus* in Fiji and *P. longirostris, H. ensifer,* and *H. laevigatus* in the Marianas.

METHODS

All shrimps examined were caught in baited traps similar to those described in previous resource surveys (e.g., King, 1981a).

The size of all shrimps was recorded as carapace length (the distance between the posterior margin of the orbit and the posterior median edge of the cephalothorax) measured to the nearest 0.1 mm.

Shrimps were sexed by an examination of the endopods of the first two pairs of pleopods and the

Table 1. Pandalid shrimps caught during deepwater trapping surveys in Fiji and the Marianas. The trap abundance of each species in each of the two locations is indicated as C (common), O (occasional), R (rare), or no letter (not found). The depth or depth range at which each species was caught is given in metres.

Species		Fiji	Marianas	Depth (m)
Parapandalus serratifrons	Pyjama shrimp	C	—	<380
*Parapandalus serratifrons***		O	—	<380
Plesionika longirostris	Stars and stripes shrimp	C	C	120–540
Plesionika rostricrescentis		R	—	240–290
Plesionika sindoi		—	R	375
Plesionika ensis	Striped gladiator shrimp*	O	R	450–640
Plesionika martia	Golden shrimp*	O	R	360–600
Heterocarpus ensifer	Armed nylon shrimp*	O	C	240–580
Heterocarpus sibogae	Mino nylon shrimp*	C	R	250–750
Heterocarpus gibbosus	Humpback nylon shrimp*	C	R	280–750
Heterocarpus lepidus		—	O	630–740
Heterocarpus laevigatus	Smooth nylon shrimp*	C	C	400–825
Heterocarpus longirostris		—	C	<825
Heterocarpus dorsalis	Madagascar nylon shrimp*	—	C	630–920

* Standard FAO name (Holthuis, 1980).
** Possibly a second form of *P. serratifrons* or a distinct species (King, in press).

basal segments of the last pair of pereiopods. The former structures are shown for *H. sibogae* in Fig. 1 and were similar in the other species studied.

The endopod of the second pleopod in males in particular was examined by using a low power microscope to measure the size of the appendix masculina as a percentage of the size of the appendix interna. Thus, scores ranged from zero (no visible appendix masculina) to close to 100 (when the appendix interna and the appendix masculina were of a similar size). This quantity was called the "relative length" of the appendix masculina.

Data from a wide size range of males were used to determine the relation between shrimp size (carapace length) and the relative length of the appendix masculina and to test the alternative hypotheses that this organ was either, (a) decreasing in size with shrimp growth (suggesting that male characteristics were degenerating and individuals were changing to female form), or, (b) increasing in size with shrimp growth (suggesting that male characteristics were developing and that individuals with reduced appendices masculinae were immature males).

RESULTS

The sex of even the smallest individuals examined in this study was easily determined by examination of the endopod of the first pleopod and the coxa of the fifth pereiopod. The shape of the endopod of the first pleopod varied somewhat with species and shrimp size (carapace length), but were always of either distinctly male or distinctly female form. Also, the male gonopores located on the coxal segments of the fifth pair of pereiopods were always present in males, though minute in the very small males, and absent in females of all sizes. These characters were consistent. The appendix masculina on the endopod of the second pleopod of males, however, underwent considerable change with shrimp growth. In very small males, the appendix masculina was absent, making the second pleopod essentially indistinguishable from that of females of the same size. These structures first appeared in developing males as small rounded buds and increased in relative length with increasing shrimp size. The distal end of the organ also became covered with an increasing number of setae in larger individuals.

The relationship between shrimp carapace length and the relative length of the appendix masculina is shown in Fig. 2 for *P. longirostris, H. ensifer, H. sibogae, H. gibbosus,* and *H. laevigatus* from Fiji and *P. longirostris, H. ensifer,* and *H. laevigatus* from the Marianas.

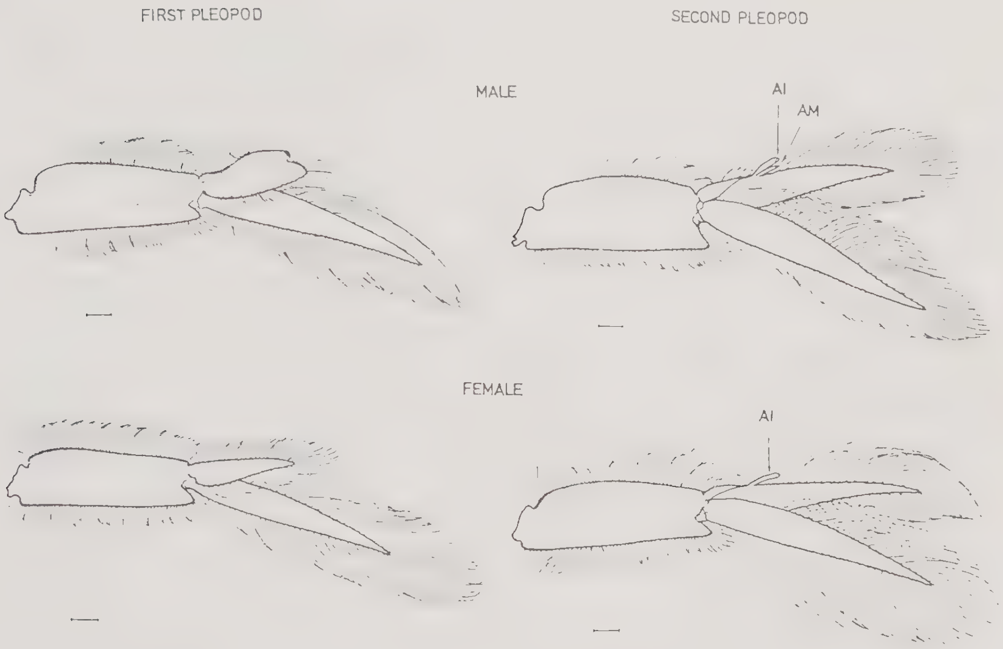

Fig. 1. *Heterocarpus sibogae.* Left: first pleopod showing male (top) and female endopod (bottom). Right: second pleopod with appendix masculina (AM) and appendix interna (AI) of male (top) and latter organ only in female (bottom). Pleopods illustrated from a 26.0-mm (carapace length) male and a 26.3-mm female. Horizontal scales indicate 1 mm.

Discussion

Morphometric evidence presented here strongly suggested that the pandalid species examined were dioecious. In previous work on tropical deepwater pandalids, authors appear to have incorrectly concluded that some of these same species were protandrous hermaphrodites. This may be because of one or several reasons including, (a) unreliable characteristics being used to determine sex, (b) the presence of a high ratio of females to males in the largest size classes, and (c) the presence of small males with reduced appendices masculinae.

Wilder (1977), in particular, stated that small females were not evident in his large samples of *H. ensifer* and *H. laevigatus* from Guam. During our investigations of shrimps from Guam and the northern Marianas Islands, however, we found that small females were common in these species and that sex ratios in small size classes were close to 1:1.

Sex ratios favouring females in larger size classes have traditionally been used as evidence for sex reversal (Wenner, 1972). Although such sex ratios were evident in some samples of shrimps obtained in our study, it should be noted that similar variations in sex ratios can occur in dioecious organisms where there are sex related differences in growth, mortality, migration, and habitat preference. In the case of animals caught by trapping, it is also possible that susceptibility to traps may differ between sexes. Sex ratios appear to have been incorrectly used to support sex reversal hypotheses in at least some other crustaceans (see Wenner and Haley, 1981).

Sex reversal is known to be common in temperate deepwater pandalids (Rasmussen, 1953; Butler, 1964). In our studies, small males with reduced appendices

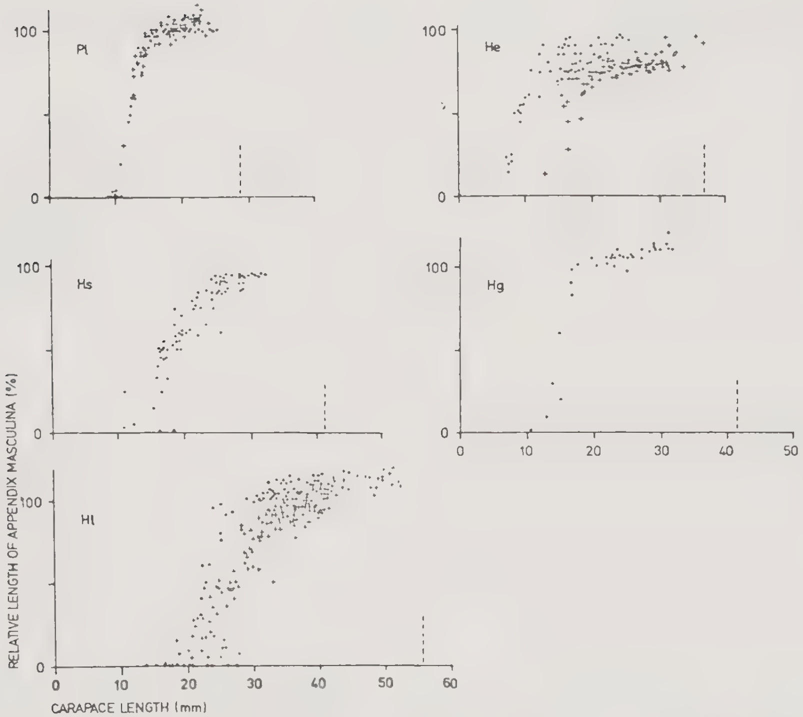

Fig. 2. Relation of relative size (%) of appendix masculina to shrimp carapace length (mm) in samples collected from Fiji (dots) and Guam (crosses). Species are Pl (*Plesionika longirostris*), He (*Heterocarpus ensifer*), Hs (*H. sibogae*), Hg (*H. gibbosus*) and Hl (*H. laevigatus*). Maximum carapace length of each species indicated by vertical broken line.

masculinae were similar, with respect to the appearance of the second pleopods, to the intersex, or transitional, individuals of these temperate species. They were, however, clearly males, based on the morphology of the previously described organs. This indicates that these individuals, in tropical pandalids, were not transitionals, but were immature and developing males. Although not all shrimp species caught during our surveys (Table 1) were analysed due to the lack of small individuals in our collections of some species, dioecy may be widespread in tropical deepwater pandalids.

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MARKS IN TOOTH DENTINE OF FEMALE DOLPHINS (GENUS *STENELLA*) AS INDICATORS OF PARTURITION

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Abstract.—In decalcified and hematoxylin-stained thin section, teeth of sexually mature female spotted dolphins (*Stenella attenuata*) often exhibit a deeply dark-stained layer (DSL) at the boundary of one or more of their annual growth layer groups. We compared DSL counts, made without reproductive information, to the corresponding reproductive condition in 75 females to test five hypotheses concerning the possible significance of DSLs. We found an exclusive association between DSLs and calving events. The teeth of an Hawaiian spinner dolphin, *Stenella longirostris*, labeled with tetracycline one month after giving birth to a calf in captivity, contained a dentinal DSL near the label. The number of DSLs in the dentine of a female probably indicates the minimum number of calves born to the female. In future studies DSL counts may be useful in estimating birth frequencies, year-specific birth rates, and calf mortality in odontocetes.

In the teeth of pinnipeds certain peculiar dentinal layers form concurrently with periods of active breeding, fasting, weaning, migration, and molting (Hamilton, 1934; Laws, 1952, 1953, 1962; Laws and Purves, 1956; Fay, 1953; Fisher, 1954; Fisher and MacKenzie, 1954; Kenyon and Fiscus, 1963; Carrick and Ingham, 1962; Scheffer and Peterson, 1967; Scheffer, 1975), although no causal relationship has been demonstrated. Klevezal' and Tormosov (1971) investigated unusually contrasting layers in the dentine of female sperm whales in an attempt to find an association between the layers and reproductive cycles, but failed to obtain clear correlations. Nevertheless, because such a connection, if established, would provide new avenues for the biological study of commercial and protected cetacean species, the search for reproductive marks in the layered hard parts of cetaceans has continued.

Annual layers or growth layer groups (GLGs, terminology of Perrin and Myrick, 1980) in dentine of toothed whales and dolphins consist of numerous layers having different optical densities, the number and contrast of which vary by age, individual, and species. Variations within a GLG are of at least two types: 1) differences in number and width of the fine layers; and 2) differences in optical contrast between the major zones. Probably, formation of the fine layers is influenced by major differences in growth patterns of the dentine, and differences in optical contrast of the major zones are due to differences in mineral content (Suchovskaya and Klevezal', 1982). With this distinction as a basis, we have assumed that the formation of fine layers, connected with lunar monthly periodicity by Laws (1962), Kasuya (1977), Myrick (1979. 1980, in press), and Hohn (1980) is associated, perhaps genetically, with the growth process, rather than with calcification. Conversely, the optical densities of broad zones within GLGs relate to changes in the mineralization process.

In some species of terrestrial mammals, formation of accessory layers in bone is caused by temporary cessation of bone growth, not by reproductive cycles (Klevezal' and Mina, 1973). Neither pregnancy nor lactation appears to alter the growth process of the skeleton or the teeth (Klevezal' and Mina, in press), but mineral content should be affected considerably during such peak periods of calcium demand.

If this is true for toothed cetaceans, then any marks connected with reproduction should be found in the major zones of dentinal GLGs in teeth of sexually mature females. The present paper reports our efforts to locate reproduction marks in the dentine of teeth of female spotted and Hawaiian spinner dolphins (*Stenella attenuata* and *Stenella longirostris*).

J. Mamm., 65(1):103–110, 1984

MATERIALS AND METHODS

Spinner dolphin.—We examined thin sections of teeth from a female spinner dolphin from Hawaii, that had been labeled with tetracycline (given as a medical treatment) one month after her calf was born. We compared the position of the label, located in the dentinal pattern in an undecalcified thin section by ultraviolet light microscopy, with its estimated position in the pattern of decalcified and stained thin sections of her teeth.

Spotted dolphins.—We examined the dentine of teeth from spotted dolphins killed incidentally in the purse-seine fishery for yellowfin tuna in the eastern tropical Pacific (Perrin et al., 1976). The teeth were prepared as decalcified and stained mid-longitudinal thin sections, 25 μm thick, and we examined them at 39 and 150× in plain transmitted light with a compound microscope. The dentine in stained thin sections shows well-developed zones of different stain intensities, which correspond to the broad zones of different optical densities in undecalcified thin sections.

First, we studied thin sections of teeth from 40 adult males and 40 adult females (ages 10–44 years) chosen arbitrarily from a random sample of 1600 specimens, the only requirement being that they were of high quality in general appearance. We found that in females the GLG boundary layers were distinctly thinner more often and more intensely stained than in males. Second, we examined 75 adult female specimens (ages 10–28 years) for which data were available regarding reproductive condition at death, to determine a possible connection between the presence of a deep stained layer (DSL) and reproductive state.

Working independently, we each determined the number and positions of DSLs, without access to the biological information of the specimens except for sex and estimated age. We resolved discrepancies in our independent results on some specimens by studying those specimens together, before accessing the reproductive data.

We formulated the following five hypotheses to test DSL relationships to reproductive condition. 1) DSLs relate to all ovulations, whether or not they result in pregnancies, or to all but the most recently fertilized ovulation. We tested this by assuming that each ovulation results in a corpus luteum (CL) that ultimately regresses to a corpus albicans (CA) and that each CA persists for life; therefore the DSL count should be equal to the total count of the CAs plus CLs. Additionally, the DSL count should be equal to CAs plus CLs excluding CLs associated with a fetus. 2) DSLs relate to pregnancy. If the gestation period for spotted dolphins is approximately one year (Perrin et al., 1976), then a DSL should occur within the last annual GLG in all pregnant females. 3) DSLs relate either to parturition or to lactation, or to both. The DSL count should be equal to or less than the count of CAs excluding any CL of an existing pregnancy, given that not all ovulations result in pregnancy and birth. 4) DSLs relate to lactation only. If lactation in non-pregnant females indicates the presence of a nursing calf, then in lactating non-pregnant females a DSL should occur in the last GLG with no space between the DSL and the pulp cavity. 5) DSLs relate to parturition only. In lactating females, a DSL should occur within the last two GLGs, given that nursing may last for one year or more in spotted dolphins (Perrin et al., 1976; Kasuya, 1976).

All 75 females used in the tests had at least one CA (range 1–13, mean 3.92). Thirty were pregnant. Forty were lactating. Three of those pregnant were lactating.

RESULTS

Definition, occurrence, and spacing of DSLs.—A DSL differed from other GLG boundary zones by being distinctly more darkly stained and thinner. It stood out from other layers along its entire longitudinal extent from apex to base (Fig. 1). Only one DSL occurred within one GLG, but one often occurred in the next adjacent GLG, or in each of the adjacent two GLGs (rarely). Often DSLs were separated by two or more GLGs. Up to five DSLs were found in a single female specimen.

Despite the identification of DSLs in males, we independently arrived at the conclusion that DSLs in males were subtly different in character from those observed in females. Nevertheless, clear distinctions between DSLs in males and in females were difficult to describe, and we have here used the same definition for both sexes.

Doubtful DSLs.—The detection of DSLs depended on the quality of resolution of layers in a thin section. We observed other layers in the adult dentine of both sexes that resembled, but were rather fainter or thicker than DSLs and were more intensely stained than the other GLG boundary layers. These we have called "doubtful" DSLs. The difference between "definite" and "doubtful" DSLs remains subjective. "Doubtful" DSLs were not included in our final counts.

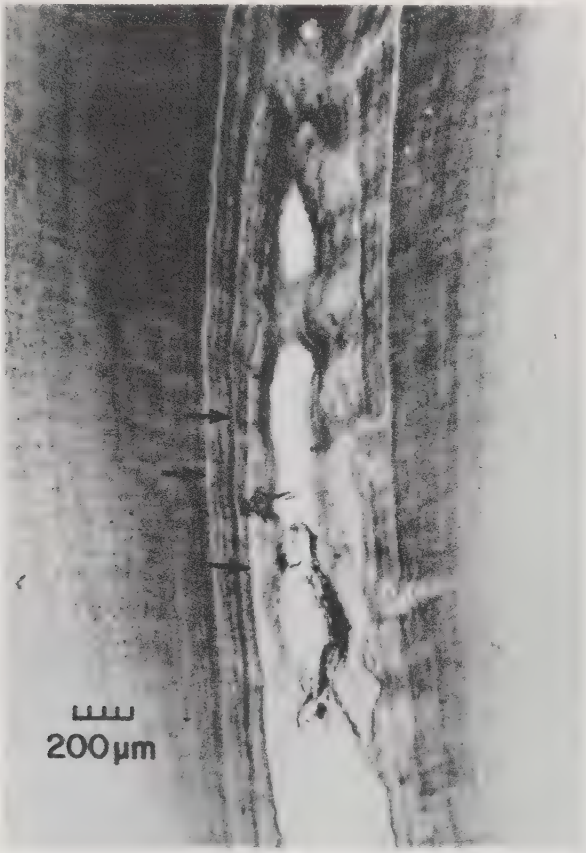

FIG. 1.—Tooth thin section from female spotted dolphin, DRD 0042, with three DSLs in dentine (arrows) (N = neonatal line).

Maturation layers.—A dark-stained boundary layer resembling a DSL, but less intensely stained and less distinct, occurred in the eight or ninth GLG in almost all males and in the sixth or seventh GLG of almost all females studied. Because they were deposited at least three years before females are known to ovulate (at 10–11 years) and before the testes of the males suddenly increase in weight (at 12 years), they were ignored in our DSL counts. We consider them to represent an attainment of some important plateau in the maturational process and we have called them maturation layers (see Fig. 2).

Comparison between DSL counts for males and females—The range of DSL totals by each of us for the 40 females was one to five. We observed DSLs in all specimens. For the 40 males, Klevezal' determined that the range was zero to two and found DSLs in only 10 specimens. The counts made by Myrick for the males ranged from 0 to 3 (3 in only one specimen) and he found DSLs in 14 specimens.

The relative number of DSLs defined as "doubtful" was considerably higher in males than in females. For males, one of us noted 12 "doubtful" with 14 "definite," the other noted 23 "doubtful" with 10 "definite." For females, one of us noted 12 "doubtful" in addition to 96 "definite" DSLs; the other noted 32 "doubtful" compared to 96 "definite."

Test of hypothesis 1: DSLs reflect ovulations.—We studied this in 75 females (Table 1, 1).

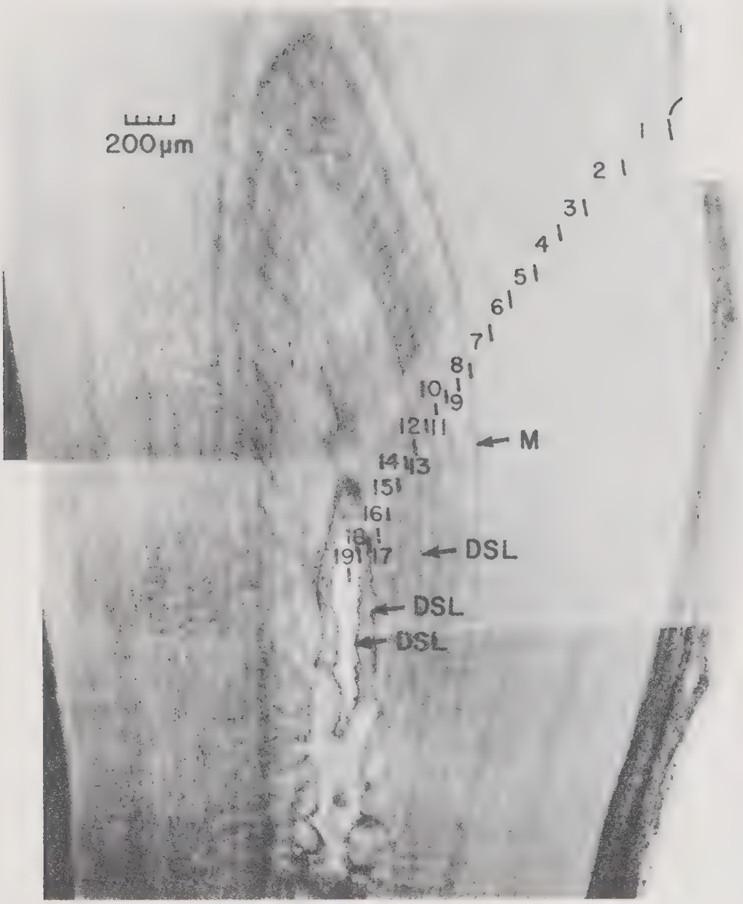

FIG. 2.—Tooth thin section from 19-year-old female spotted dolphin, FBG 0030. Arrows indicate maturational layer (M) at end of seventh year, DSLs at end of 12th, 17th, and 18th dentinal GLGs.

In 65 cases, the DSL count was less than the number of CAs plus CLs. In 10 females the DSL count was equal to the CA plus CL count (Table 1, 1a). When CLs associated with fetuses (30) were excluded from each count, 58 of the females had a DSL count less than the CA count and 17 had equal numbers of DSLs and CAs (Table 1, 1b). If DSLs reflect all ovulations, or if DSLs reflect all ovulations except those represented by the last formed pregnancy, the DSL counts should have been equal to the CA and/or CA + CL counts. The hypothesis was not sustained.

Test of hypothesis 2: DSLs reflect pregnancies.—This was studied in the 30 pregnant females (Tables 1, 2). A DSL was detected in the last GLG in only one individual. She was pregnant and lactating at the time of death. If DSLs reflect pregnancies, all 30 pregnant females should have had a DSL in the last GLG. The coincidence test was negative (Table 1, 2a).

Test of hypotheses 3, 4, and 5: DSLs reflect parturition and/or lactation.—We tested hypothesis 3 in 75 specimens. DSL counts were equal to or less than the number of CAs plus CLs, excluding CLs of pregnancy, for corresponding specimens in 70 cases (Table 1, 3a). In 25 of the 30 pregnant females DSL counts were less than the CAs plus CLs of pregnancy (Table 1,

TABLE 1.—*Percent coincidence tests of five hypotheses of relationships between DSLs and reproductive condition in 75 female spotted dolphins,* Stenella attenuata. *DSL, deep stained layer; GLG, growth layer group.*

Hypotheses: formation of DSL associated with	Tests of coincidence	Total number of specimens	Coincidence		Noncoincidence		Result of test
			Number of specimens	Percent	Number of specimens	Percent	
1 Ovulation							
a. all ovulations	1a. DSL count = CAs + CLs	75	10	13	65	87	Negative
b. all but most recent fertilized ovulation	1b. DSL count = CAs + CLs excluding CLs of pregnancy	75	17	22	58	78	Negative
2. Pregnancy	2a. In all pregnant females, DSL in last GLG	30	1	3	28	97	Negative
3 Parturition or lactation	3a. DSL count ≤ CAs + CLs excluding any CLs of pregnancy	75	70	93	5	7	Positive
	3b. In all pregnant females, DSL count < CAs + CLs of pregnancy	30	25	83	5	7	Positive
4. Lactation only	4a. In all lactating females, DSL in last GLG without a space between DSL and pulp cavity	40	0	0	40	100	Negative
5. Parturition only	5a. In all lactating females, at least one DSL within the last two GLGs.	40	35	88	5	12	Positive

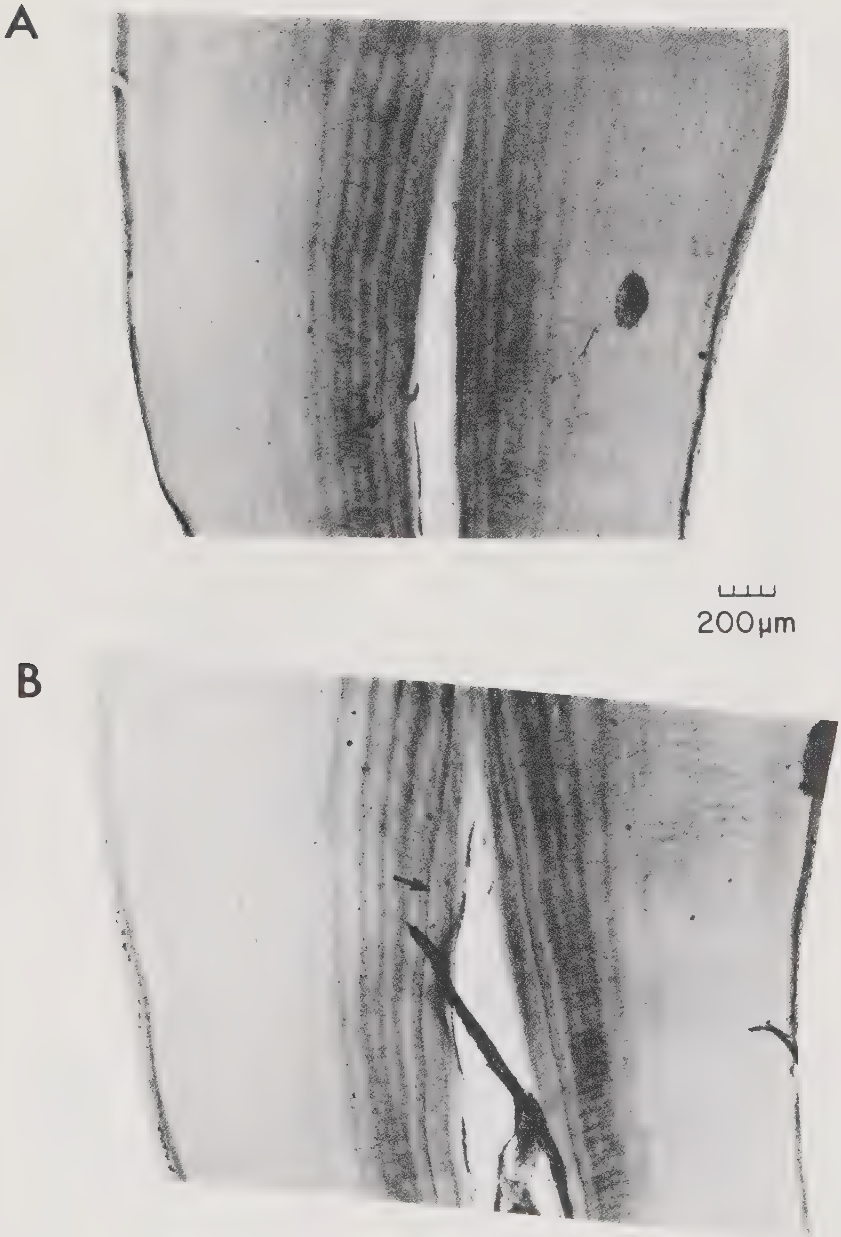

FIG. 3.—Thin sections of two teeth (A and B) from female Hawaiian spinner dolphin labeled with tetracycline one month after giving birth to calf in captivity. DSL (arrows) occurs in dentine at same position in both teeth, immediately external to label observed in untreated thin sections under ultraviolet light.

3b). The highly positive test results of this hypothesis permitted us to test hypotheses 4 and 5 separately.

We tested hypothesis 4, that DSLs reflect lactation exclusively (Table 1, 4) in 40 lactating specimens. In no case was a DSL observed in the last GLG without a space between the DSL and the pulp cavity (Table 1, 4a). Only seven of the 40 had a DSL in the last GLG. If DSLs are indicators of lactation, we should have found a DSL in each last-formed GLG with no separation from the plup cavity.

We tested hypothesis 5, that DSLs reflect parturition only (Table 1, 5) in 40 lactating females. Thirty-five had a DSL within the last two GLGs (Table 1, 5a). In seven cases a DSL was present in the last GLG and in 28 cases one was found in the next-to-last GLG. Because parturition occurs a year or more before nursing is thought to cease in spotted dolphins (Perrin et al., 1976; Kasuya, 1976), a DSL should be present in either the last or next-to-last GLG in lactating females if DSLs are indicators of parturition. A highly positive result was obtained in this test.

Captive female Hawaiian spinner dolphin.—In this individual's teeth, we found only one distinct DSL (Fig. 3). The DSL was situated adjacent to the position of the tetracycline label introduced soon after the calf was born.

DISCUSSION

Assuming that DSLs reflect parturitions exclusively, exceptions to the positive results must be addressed. In 12% of the lactating females no DSLs occurred within the last two GLGs (Table 1, 5a). In identifying DSLs near the pulp cavity it was not always easy to determine precisely which GLG they occupied. GLGs near the pulp cavity in adult specimens are thin (40–50 μm thick) and commonly their complete patterns are not fully stained. In our opinion, much of the error in determining the precise positions of the DSLs stems from the problem of GLG resolution.

It is more difficult to explain why 17 out of 35 nonlactating females, pregnant and nonpregnant, had DSLs in the last two GLGs. Although some of the problem may have been due to imprecision in GLG delimitation, we think that many of these females may have lost their calves after birth and ceased lactating.

Eight of the 75 females had between 9 and 13 CAs, but the greatest number of DSLs counted was five (in a 17-year-old with seven CAs). We would have expected a proportional increase of DSLs with an increase in scars and we are unable to explain why such a result was not obtained. It is possible that CAs and parturitions may not be significantly correlated, i.e., the proportion of CAs representing eventual pregnancy and birth may be quite irregular (S. Reilly, NMFS, pers. comm., 1982). Perhaps DSLs are not always recorded with equal clarity in later-deposited dentine and we may have failed to detect some of the DSLs in the older specimens. We assume that the DSL counts represent a minimum of the actual calving episodes.

Proportionately fewer DSLs (mode = 0) were found in the random sample of adult males (17–25%, range 1 to 3) than females (100%, mode = 2, range 1 to 5). We are unable to explain, at this time, why DSLs occur in males, but note that "DSLs" in males appear to be of a different nature than those in females. In any case, their presence in males does not invalidate the highly consistent association of DSLs with births in females.

At present there is no basis for rejecting the hypothesis that DSLs reflect parturitions exclusively. Further work is required on larger samples in which the sex of the specimens is not known to the investigator during DSL identification. More precise distinctions of DSLs between males and females is necessary. A more objective description of DSLs in females is needed to minimize discrepancies in DSL counts. Similar marks should be sought in teeth of toothed cetaceans other than *Stenella* spp. With validation and refinement of the method, DSLs may prove to be a useful tool in future studies of the reproductive biology of toothed whales and dolphins. They may be used in estimating the frequency of births, extrapolating year-specific birth rates, and estimating calf mortality rates.

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Albacore tuna catch distributions relative to environmental features observed from satellites

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Abstract—Albacore tuna catch data from the summer of 1981 are displayed on concurrent satellite images of sea surface temperature and phytoplankton pigment concentration, from the NOAA-7 Advanced Very High Resolution Radiometer (AVHRR) and the Nimbus-7 Coastal Zone Color Scanner (CZCS), respectively. During 3 week-long periods off California, intense fishing activity and larger catches, indicating aggregations of albacore, were located within pockets of warm, blue oceanic water intruding into the boundary between oceanic and cooler greenish coastal waters. A relatively productive oceanic region, defined by a color front visible in a CZCS image, was the site of albacore aggregation in waters several hundred miles offshore during the first 2 weeks of September 1981.

INTRODUCTION

ALBACORE, *Thunnus alalunga*, is a highly migratory tuna that supports important United States commercial and recreational fisheries and several foreign fisheries in the North Pacific. Albacore are found off the coast of North America from central Baja California to British Columbia, Canada, from late spring to autumn.

The migration, distribution, availability, and catchability of albacore are markedly influenced by oceanographic conditions in the North Pacific, notably hydrographic fronts. For example, albacore fishing grounds in the western Pacific have been linked to oceanic fronts in the region of the Kuroshio current and Kuroshio Extension waters (UDA, 1973). Seasonal migration into North American coastal waters is associated with the Transition Zone and its frontal boundaries (LAURS and LYNN, 1977). Coastal upwelling fronts and fronts at the margin of river plumes influence local concentrations and movements of albacore in United States coastal waters (PEARCY and MUELLER, 1970; LAURS *et al.*, 1977). Albacore fishermen traditionally fish blue, oceanic waters warmer than 15°C and near fronts indicated by temperature or water color ‘breaks’. Fishing grounds are often found associated with undersea topographic features, such as seamounts and banks, which are believed to be sites of local enrichment and food abundance (DOTSON, 1980; SUND *et al.*, 1981).

Optimum temperature ranges for albacore catch have been determined from commercial or research vessel catches and sea surface temperature measurements (ALVERSON, 1961; CLEMENS, 1961). However, documentation of an association between albacore and thermal

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or color fronts has not been possible due to the difficulty of obtaining concurrent catch and hydrographic data covering sufficiently large areas. LAURS *et al.* (1977) used a different approach by sampling a small area around single albacore located by ultrasonic tracking and observed movements constrained by local temperature boundaries. Early attempts to detect environmental limits on tuna distributions from aircraft and satellites had some limited success (PEARCY and MUELLER, 1970; STEVENSON and MILLER, 1974).

Earth-orbiting satellites flown since 1978 rapidly provide data yielding images of sea surface temperature and the turbidity and phytoplankton pigment concentration of near-surface waters over large areas of the ocean. Some of the data are used to provide west coast fishermen with sea surface temperature and ocean color boundary charts (BREAKER, 1981; MONTGOMERY, 1981), although the benefits of such services have not yet been rigorously evaluated. This paper will show that environmental features observed in satellite i.r. and color images of the sea surface define boundaries for albacore aggregations and optimum fishing regions indicated by daily catch data.

METHODS

Concurrent satellite and fish catch data were obtained through a unique information network involving the cooperation of the Scripps Institution of Oceanography Satellite Oceanography Facility (SSOF), the Scripps Visibility Laboratory, the National Marine Fisheries Service, the California Department of Fish and Game, and the Oregon Department of Fish and Wildlife (Fig. 1). Coastal Zone Color Scanner (CZCS) data were received at the SSOF directly from the Nimbus-7 satellite and processed at the Visibility Laboratory. Data from three passes over coastal waters off California and one pass covering a region offshore of Oregon and Washington were obtained during periods of heavy fishing activity in August and September 1981 (Fig. 2). Two of the passes over coastal waters had been used to produce experimental ocean color boundary charts for distribution to a limited number of fishermen (MONTGOMERY, 1981).

Band 1 (blue) and Band 3 (green) radiances were corrected for Rayleigh and aerosol scattering by a Visibility Laboratory-modified version of the CZCS Nimbus Experimental Team's atmospheric algorithm (SMITH and WILSON, 1981). We converted the blue : green color ratio to phytoplankton pigment concentration using the pigment algorithm by CLARK (1981). Pigment values are not comparable between images due to ongoing modifications of the atmospheric algorithm during the months when the images were processed. The principal source of uncertainty was the progressive decay in the CZCS's radiometric sensitivity. The decay was known but poorly quantified when the images were processed. The coastal images are one-half normal resolution with only one of every 2 × 2-block of pixels retained, so that each pixel represents an area with dimensions of 1.6 km. The offshore image is one-third normal resolution (2.4 km).

NOAA-7 Advanced Very High Resolution Radiometer (AVHRR) i.r. data corresponding to the CZCS images were obtained from satellite passes archived at the SSOF. Channel 4 (10.5 to 11.3 μm) and Channel 5 (11.5 to 12.5 μm) radiances were converted to temperature using an SSOF radiometric calibration procedure based on LAURITSON *et al.* (1979). Sea surface temperatures corrected for atmospheric effects were estimated using the split-window algorithm proposed by MCCLAIN *et al.* (1983). Finally, the sea surface temperature images were registered to ground control points taken from the ocean color images, so that the earth locations of the two images are identical.

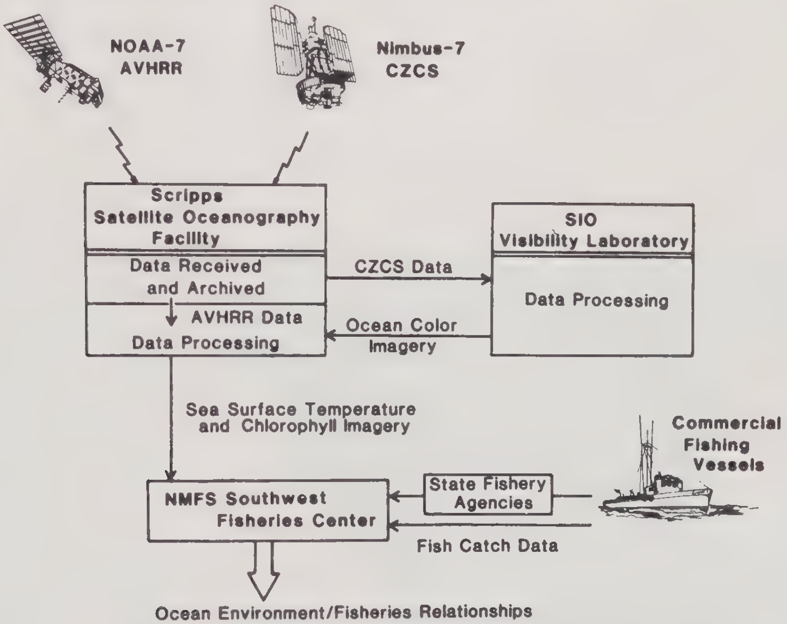
NOAA-7
AVHRR
Nimbus-7
CZCS
Scripps Satellite Oceanography Facility
Data Received and Archived
AVHRR Data
Data Processing
CZCS Data
Ocean Color Imagery
SIO Visibility Laboratory
Data Processing
Sea Surface Temperature and Chlorophyll Imagery
Commercial Fishing Vessels
State Fishery Agencies
NMFS Southwest Fisheries Center
Fish Catch Data
Ocean Environment/Fisheries Relationships

Fig. 1. Satellite data collection and processing network utilized by the National Marine Fisheries Service, Southwest Fisheries Center.

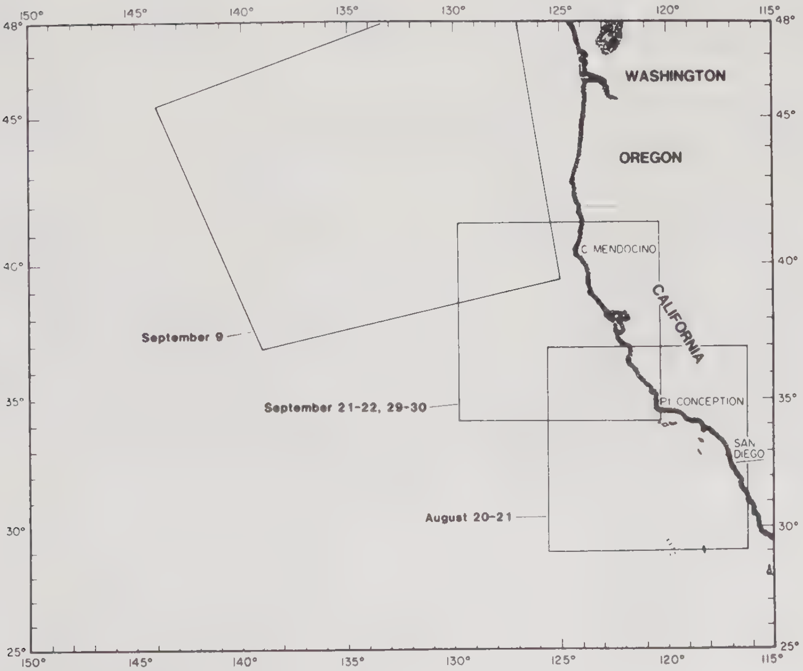
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Fig. 2. Locations of satellite images.

Albacore catch data were obtained from daily logs submitted by fishermen (LAURS *et al.*, 1975). Positions were usually recorded at the start of a day's fishing activity, which may cover up to 50 km. Catches were normalized to 150 line-hours, a typical full day of effort by an albacore trolling or jig boat. Catch data for periods from 2 days before to 2 days after each pair of satellite passes were plotted on the satellite temperature and phytoplankton pigment images. The offshore catch data (1 to 15 September 1981) are means from 1° squares. Fishing boats do not randomly sample the albacore population; there is communication among boats and a fleet will aggregate in productive fishing regions, based on current fishing success and traditional indicators such as water temperature, color, sea bird activity, etc.

The AVHRR images presented here are enhanced so that sea surface temperature ranges from warm (nearly black) to cold (nearly white). The CZCS images are false-color enhanced. Land is masked with black, while clouds appear white in the SST images and black in the chlorophyll images. The grey and color scales are not consistent between images, in order to optimally define ocean features.

RESULTS

In Fig. 3 (20 to 21 August) a coastal water mass characterized by low temperature (<15°C) and high phytoplankton pigments (>0.60 mg m^{-3}) was evident north of Pt. Conception. The large plume of this water extending offshore to the south was a feature present for most of the year in the region. Fishing activity during 18 to 23 August was concentrated east of the plume in warm (>16°C) and blue (<0.30 mg pigments m^{-3}) oceanic water, as measured from the satellites. Only small catches were reported within the coastal water plume. The largest catches were in two pockets of oceanic water on the eastern edge of the plume. In the northern pocket (not covered by the CZCS image), large catches were located close to the thermal front at the oceanic-coastal boundary. Fishing activity in the northern pocket peaked on 20 August, while activity in the southern pocket peaked on 17 August. Eastward movement of the southern pocket between 17 August and the satellite passes may explain the greater apparent separation between fishing activity and the front.

In Fig. 4 (21 to 22 September) and Fig. 5 (29 to 30 September), an intense and meandering frontal boundary extended south from Cape Mendocino, possibly associated with upwelling there and off Pt. Arena to the south. The SST and color fronts correspond almost exactly, although the 29 September color front was more diffuse than the 30 September SST front. Differences between concurrent images are due primarily to displacement of small-scale features and to the linear enhancement algorithms. The basic pattern of the front changed slightly over the 1-week period between the two sets of images. Note the changes in the shapes of the two pockets of warm, low-pigment water just south of Cape Mendocino. During 19 to 24 September and 27 September to 2 October, fishing boats were aggregated and took the largest catches in these two pockets of oceanic water. Some small catches were reported on the coastal side of the front and within the narrow cold-water plume northwest of Cape Mendocino.

Figure 6 (9 September) covers a large oceanic region off the coasts of Washington and Oregon (Fig. 2). Sea surface temperature increased gradually from 12°C at 48°N to 20°C at 40°N, and no temperature fronts were visible in the AVHRR image. However, a diffuse and broken color front is apparent in the center of the CZCS image. The oceanographic boundary defined by the color front marks an area of high fishing activity and large mean

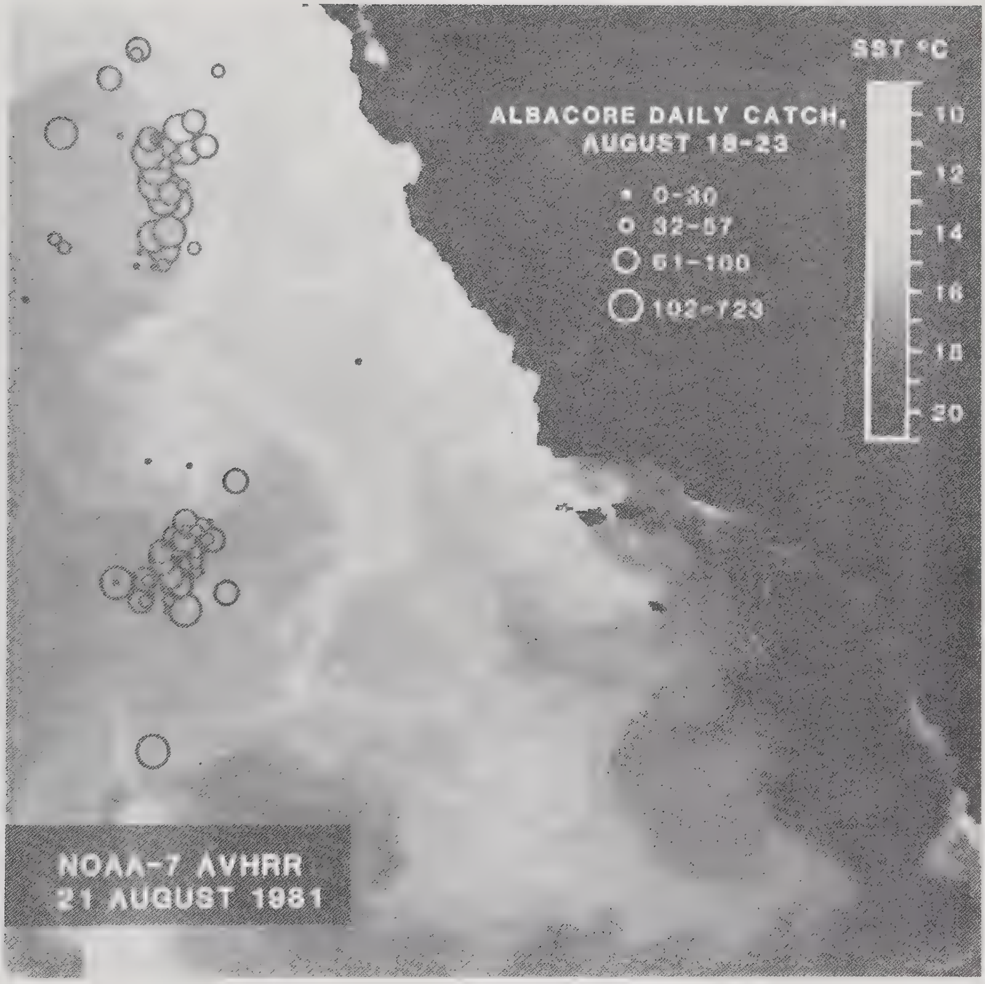

SST °C
10
12
14
16
18
20
ALBACORE DAILY CATCH,
AUGUST 18-23
0-30
32-57
51-100
102-723
NOAA-7 AVHRR
21 AUGUST 1981

Fig. 3(a)

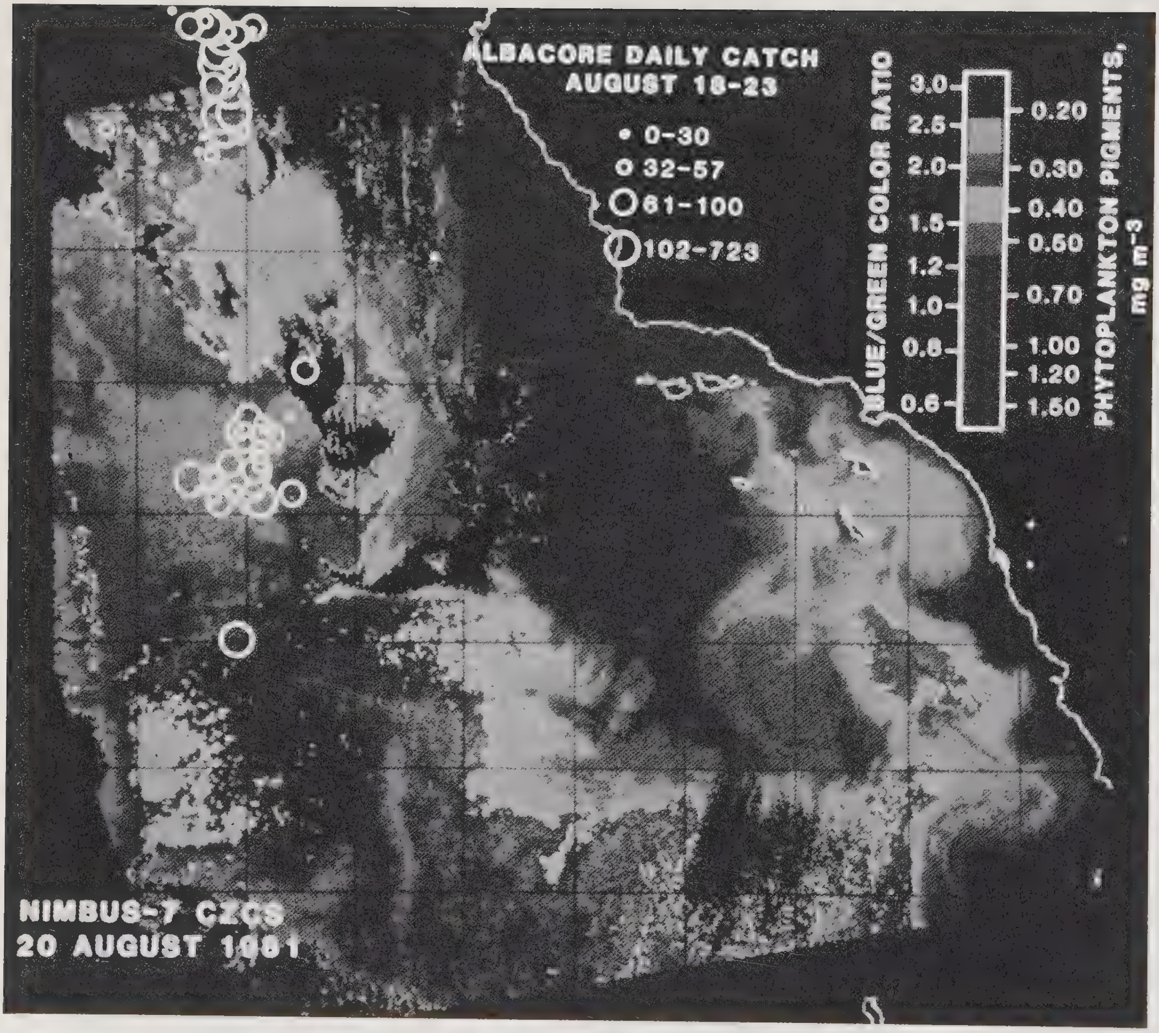

ALBACORE DAILY CATCH
AUGUST 18-23
• 0-30
o 32-57
○ 61-100
◯ 102-723
BLUE/GREEN COLOR RATIO
3.0
2.5
2.0
1.5
1.2
1.0
0.8
0.6
0.20
0.30
0.40
0.50
0.70
1.00
1.20
1.50
PHYTOPLANKTON PIGMENTS, mg m-3
NIMBUS-7 CZCS
20 AUGUST 1981

Fig. 3. Southern California daily albacore catches, 18 to 23 August 1981. (a) NOAA-7 AVHRR sea surface temperature, 21 August 1981, 0436 PST. (b) Nimbus-7 CZCS blue:green color ratio and phytoplankton pigment concentration, 20 August 1981, 1114 PST.

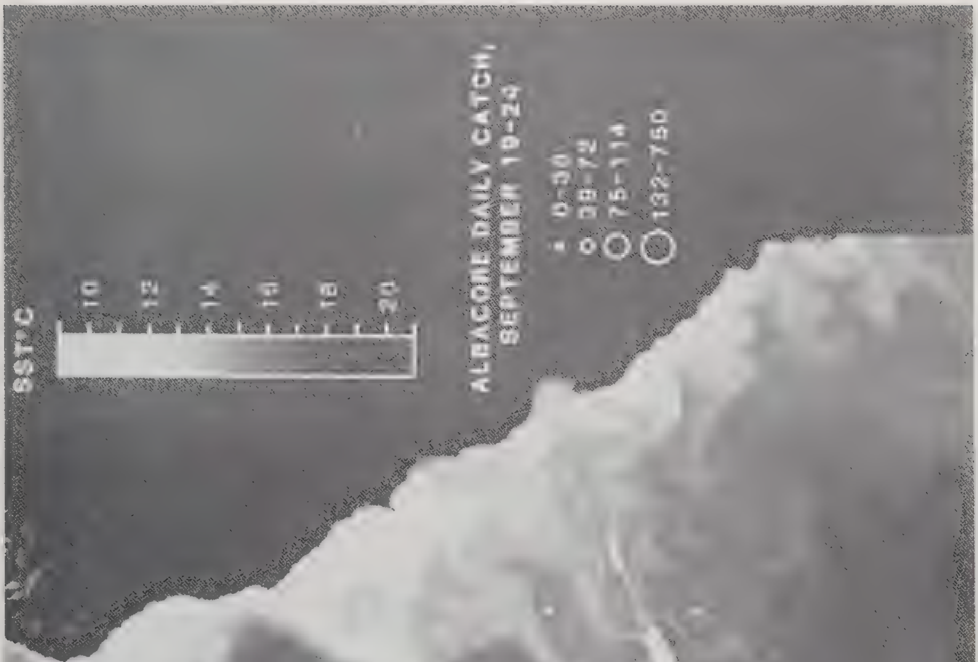

SST°C
10
12
14
16
18
20
ALBACORE DAILY CATCH,
SEPTEMBER 19-24
0-30
38-72
75-114
132-750
NOAA-7 AVHRR
21 SEPTEMBER 1981

Fig. 4(a)

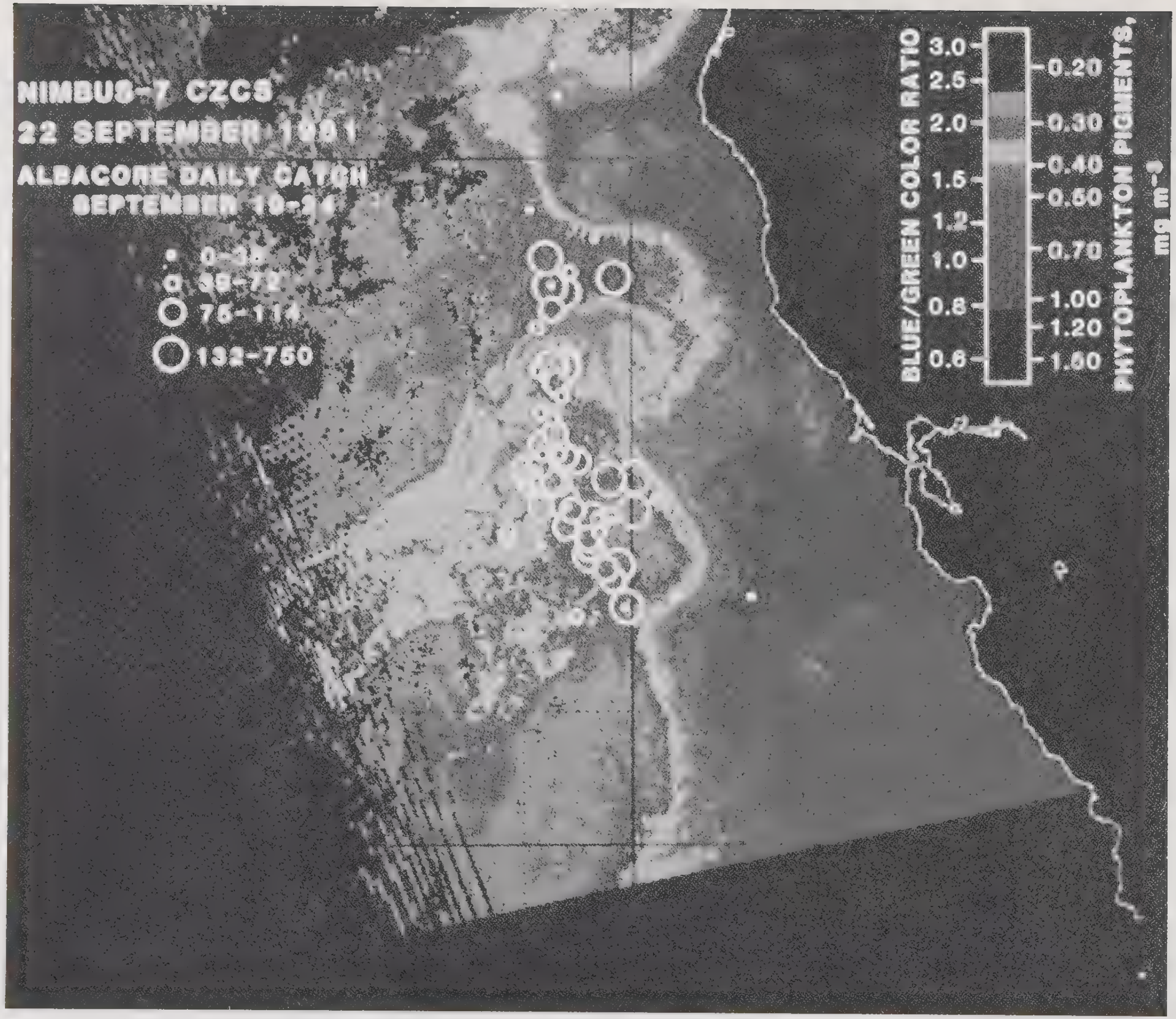

NIMBUS-7 CZCS
22 SEPTEMBER 1981
ALBACORE DAILY CATCH
SEPTEMBER 19-24
0-36
39-72
75-114
132-750
BLUE/GREEN COLOR RATIO
3.0
2.5
2.0
1.5
1.2
1.0
0.8
0.6
0.20
0.30
0.40
0.50
0.70
1.00
1.20
1.50
PHYTOPLANKTON PIGMENTS, mg m^{-3}

Fig. 4. Central California daily albacore catches, 19 to 24 September 1981. (a) NOAA-7 AVHRR sea surface temperature, 21 September 1981, 1403 PST. (b) Nimbus 7 CZCS blue : green color ratio and phytoplankton pigment concentration, 22 September 1981, 1104 PST.

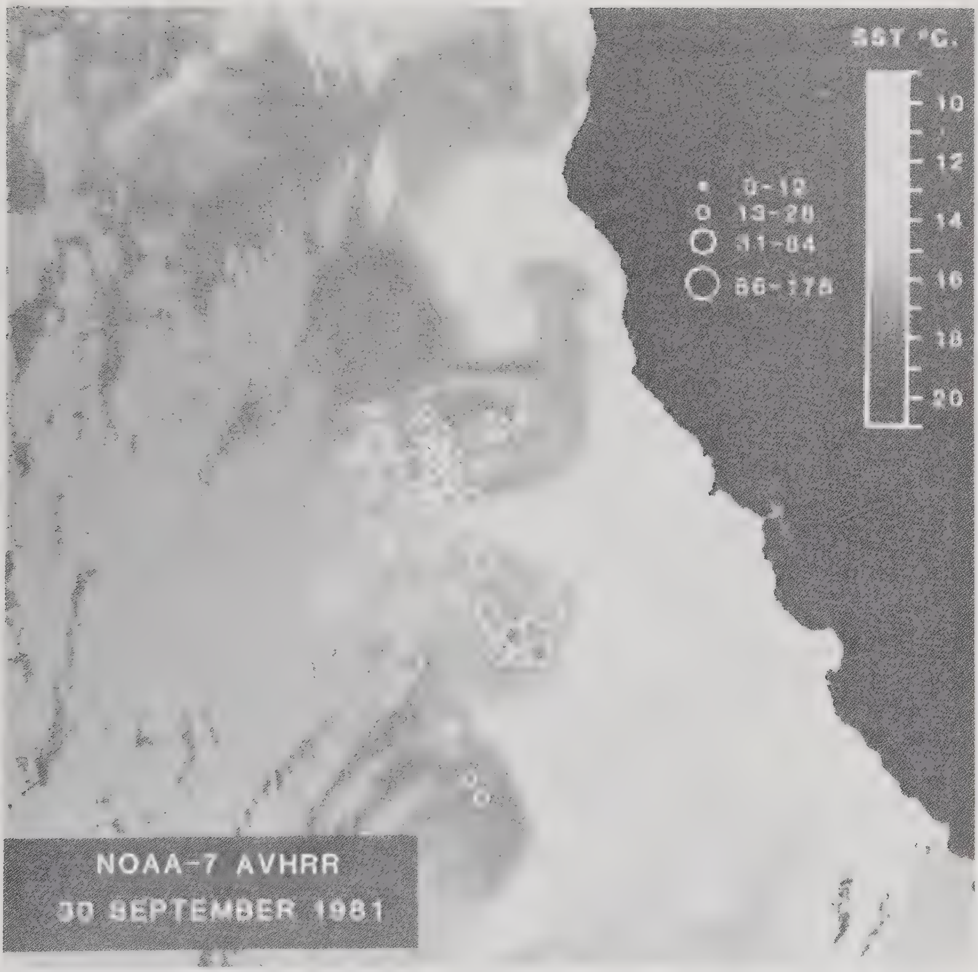

SST °C.
10
12
14
16
18
20
0-12
13-20
21-64
66-178
NOAA-7 AVHRR
30 SEPTEMBER 1981

Fig. 5(a)

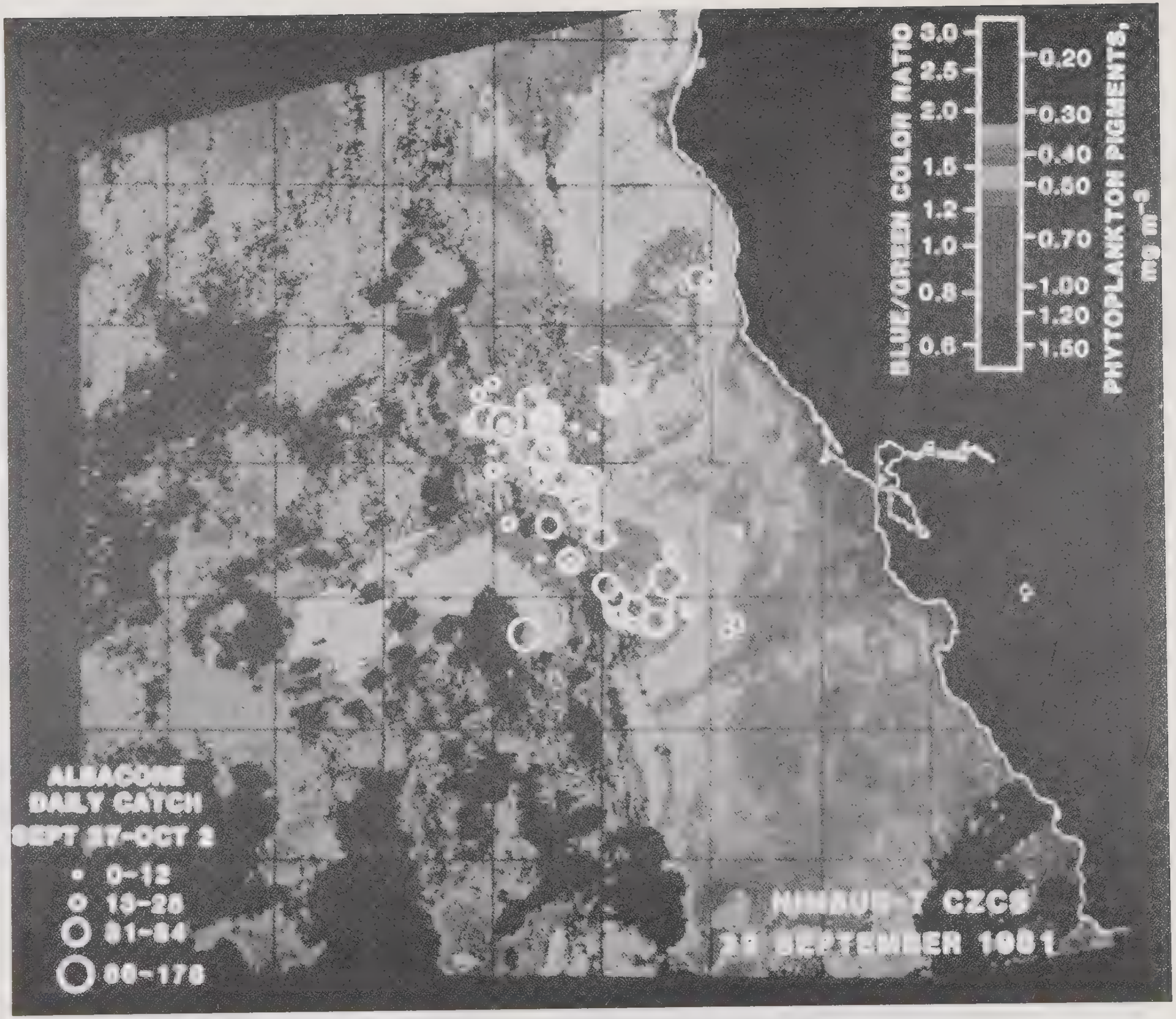
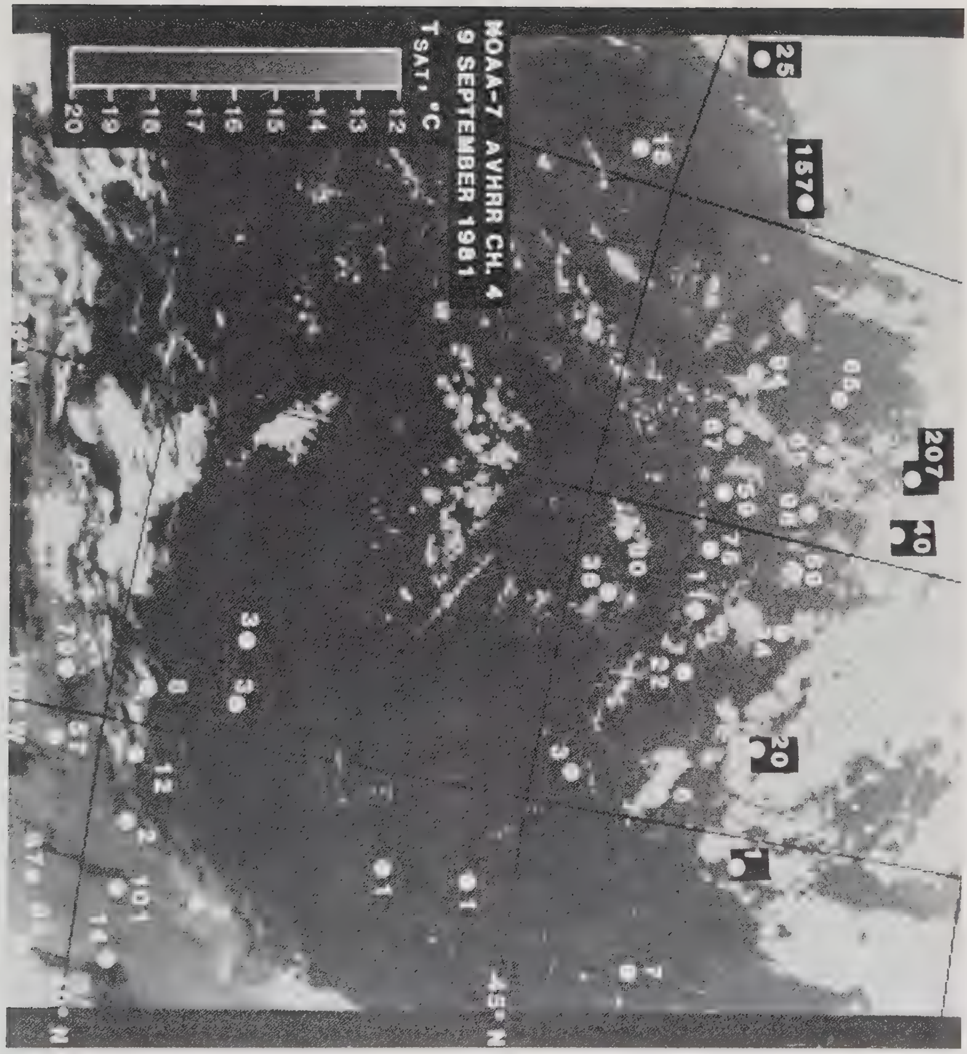

BLUE/GREEN COLOR RATIO
3.0
2.5
2.0
1.5
1.2
1.0
0.8
0.6
0.20
0.30
0.40
0.50
0.70
1.00
1.20
1.50
PHYTOPLANKTON PIGMENTS, mg m^{-3}
ALBACORE
DAILY CATCH
SEPT 27–OCT 2
0–12
13–30
31–84
85–178
NIMBUS-7 CZCS
29 SEPTEMBER 1981

Fig. 5. Central California daily albacore catches, 27 September to 2 October 1981. (a) NOAA 7 AVHRR sea surface temperature, 30 September 1981, 1402 PST. (b) Nimbus-7 CZCS blue : green color ratio and phytoplankton pigment concentration, 29 September 1981, 1130 PST.


NOAA-7 AVHRR CH. 4
9 SEPTEMBER 1981
T SAT, °C
12
13
14
15
16
17
18
19
20
45° N
157
207
25
40
20

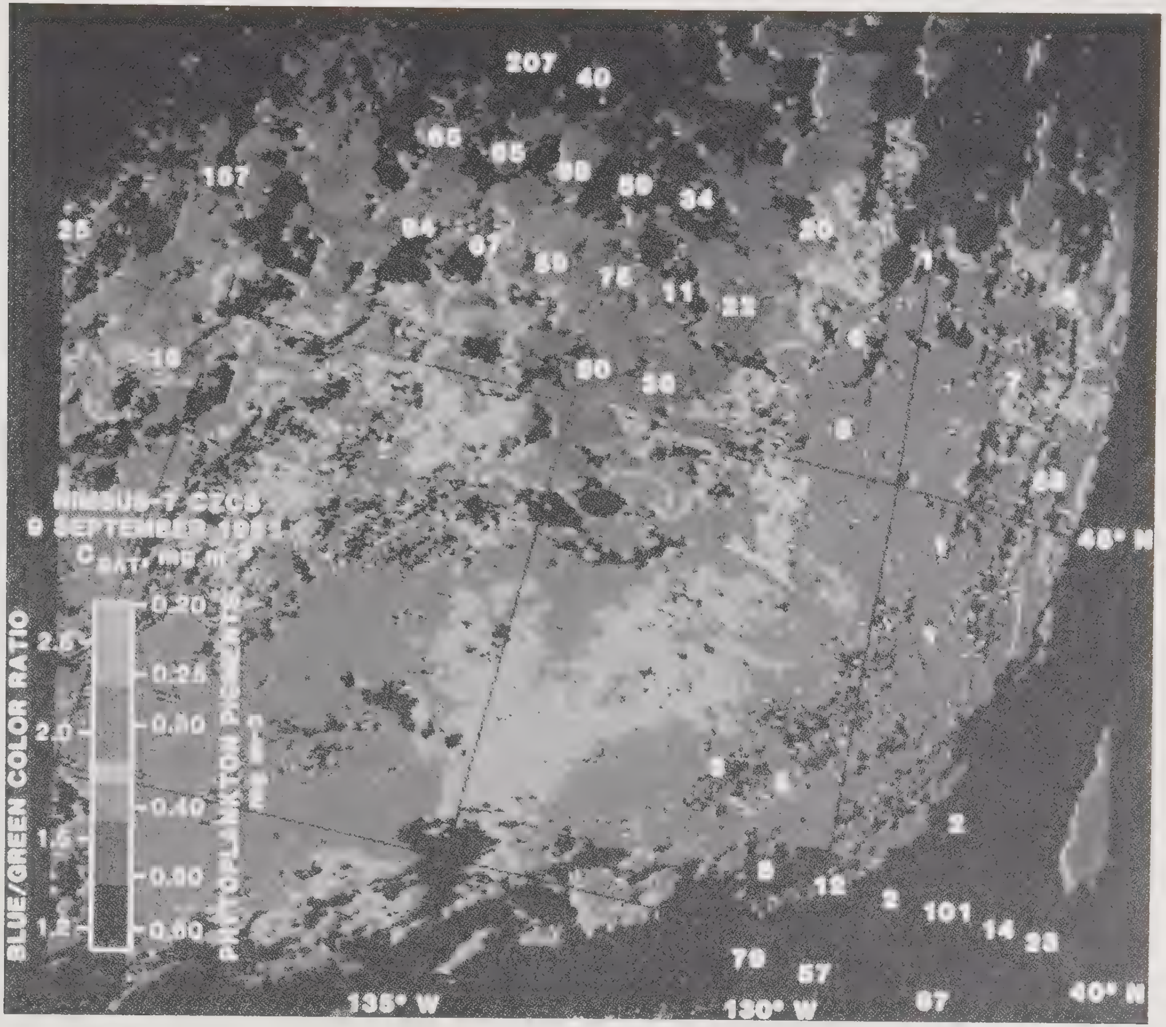

NIMBUS-7 CZCS
9 SEPTEMBER 1981
C SAT, mg m-3
BLUE/GREEN COLOR RATIO
2.5
2.0
1.5
1.2
0.20
0.25
0.30
0.40
0.60
0.80
PHYTOPLANKTON PIGMENTS
mg m-3
207
40
65
65
90
59
34
167
25
94
97
59
75
11
23
20
1
10
6
80
30
7
8
68
45° N
2
8
12
2
101
14
23
79
57
87
135° W
130° W
40° N

Fig. 6. Mean daily albacore catches in one degree squares, 1 to 15 September 1981. (a) NOAA-7 AVHRR sea surface temperature, 9 September 1981, 1438 PST. (b) Nimbus-7 CZCS blue:green color ratio and phytoplankton pigment concentration, 9 September 1981, 1215 PST.

catches in relatively productive water. The concentration of fish in the lower right corner of the images, in a region obscured by clouds, was near the coast of northern California and most likely represents the same type of aggregation observed in the coastal images.

DISCUSSION AND CONCLUSIONS

The satellite images and concurrent albacore catch data clearly show that the distribution and availability of albacore are related to oceanic fronts. They also substantiate the conventional wisdom of many fishermen who use temperature or color 'breaks' to locate potentially productive fishing areas for albacore. Our results show that in nearshore regions commercially fishable aggregations of albacore are found in warm, blue oceanic waters near temperature and color fronts on the seaward edge of coastal water masses. Relatively intense fronts are favored, such as those associated with persistent upwelling (Laurs *et al.*, 1977). We have also demonstrated for the first time that shoreward intrusions of oceanic water are particularly favorable sites for albacore aggregation.

Our results also show that in offshore waters during late summer, commercial concentrations of albacore are associated with oceanic boundaries marked by color fronts detectable from satellites but without sea surface temperature gradients. The availability of albacore in offshore waters appears to be higher in relatively productive waters. The temperature characteristic denoting the boundaries of the relatively more productive waters, if present earlier, may be lost due to seasonal warming. However, the color gradient pattern is conserved.

Explanations for the environmental preferences of albacore are changing as new knowledge is acquired. Past studies stressed confinement to a physiologically optimum temperature range (Thompson, 1917; Sund *et al.*, 1981) or utilization of frontal gradients for thermoregulation (Neill, 1976). However, temperature by itself cannot explain the observed distributions. Recent evidence based on acoustic tracking experiments conducted in conjunction with vertical temperature measurements shows that albacore move vertically through the thermocline and experience temperature changes of 5°C or more in 10 to 30-min periods (Laurs, 1983).

Albacore are believed to migrate to exploit the high densities of food organisms available in North American coastal waters. Albacore are opportunistic carnivores and consume northern anchovy, saury, euphausiids, squid, and decapod shrimp off California (Pinkas *et al.*, 1971). Suboptimum temperatures may limit them to the edges of the productive coastal water mass where such organisms are most abundant. Blackburn (1969) showed that both water temperature >20°C and abundance of suitable food are necessary conditions for the aggregation of yellowfin and skipjack tunas off Baja California. Like all tunas, the albacore is a visual predator (Magnuson, 1963). The aggregation of albacore in clear water on the oceanic side of fronts in nearshore areas may reflect an inability to efficiently capture large, mobile prey in turbid coastal water (Murphy, 1959) and a dependence on food that has migrated or been dispersed across the coastal-oceanic boundary. In offshore regions, the aggregation of albacore in relatively productive waters presumably occurs because relatively higher amounts of food organisms are present, yet the waters are clear enough for the albacore to detect them.

We have shown that both i.r. and visible color data from satellites can define environmental limits on the spatial distribution of fishable aggregations of albacore and can do so more effectively than ship or aircraft data as used in the past. Satellite images readily resolve oceanic features with dimensions of scale >100 km; no other observational perspective so convincingly reveals the shapes, sizes, and continuity of such features. Phytoplankton pigment concentration or turbidity must be at least as important as temperature in explaining and predicting the seasonal migration of albacore to the North American coast for feeding and their local aggregation near productive waters. The oceanic images covering the offshore fishery later in the season illustrate a case in which sea surface temperature patterns cannot explain the catch distribution. While the CZCS image clearly shows an important color boundary, surface temperature gradients are nonexistent after the onset of seasonal warming. With the present results, we cannot rule out the possibility that subsurface temperature gradients may be associated with such surface color features. The continued presence of a color scanner in space is critical to the further development and use of such information in fisheries research, management, and exploitation.

Acknowledgements—This work was supported in part by the National Aeronautics and Space Administration, Order W15,334. We are grateful for the assistance provided by R. Austin and R. Wittenberg at the Scripps Institution of Oceanography Visibility Laboratory, W. Perkins at the Western Fishboat Owners Association, and the many commercial albacore fishermen who kept log-book records.

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8453

GROWTH OF JACK MACKEREL, *TRACHURUS SYMMETRICUS*, IN CAPTIVITY

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ABSTRACT

Fishery data indicate that jack mackerel captured from inshore waters are seldom more than 380 mm in fork length (FL). This laboratory study shows that the inshore fish have the potential to grow as large as 425-450 mm FL. During a 2-year period laboratory-held mackerel grew more than three times faster in length and more than five times faster in weight than fish in the wild. Most of the surplus weight (65%) was fat, but a significant portion (26%) was fat-free dry weight, indicating that protein as well as fat was stored. The high levels of fat and protein accumulated by the laboratory fish indicate that the growth in length (skeletal growth) may have been near the maximum rate. The excess fat was deposited in the red and white muscles and viscera in different proportions.

RESUMEN

Los datos de pesca indican que los *Trachurus symmetricus* capturados en aguas costeras raramente alcanzan más de 380 mm de longitud a la horquilla. Los estudios en el laboratorio señalan que los peces costeros tienen un potencial de crecimiento que llega a los 425-450 mm de longitud de horquilla. Los charritos mantenidos en el laboratorio durante dos años, incrementaron su longitud y peso con una rapidez tres y cinco veces mayor respectivamente, que los peces que habitan su medio natural. La mayor parte del exceso en peso estaba constituido por grasas (65%) pero una porción significativa (26%) corresponde a peso seco sin grasas, lo cual indica que almacenan tanto proteínas como grasas. Los altos niveles de grasa y proteínas acumulados por los peces mantenidos en el laboratorio indican que el crecimiento en longitud (crecimiento del esqueleto) debió alcanzar un valor cercano a la tasa máxima de crecimiento. El exceso de grasa se depositó en diferentes proporciones en los musculos blancos y rojos, y en las vísceras.

INTRODUCTION

Reports by MacCall et al. (1980) and MacCall and Stauffer (1983) on the biology of the jack mackerel, *Trachurus symmetricus*, indicate that little is known about the structure of the jack mackerel population. The reports state that the catch consists of two size groups; the inshore purse seine fishery off southern California takes fish ranging from 100 to 300 mm FL, whereas the offshore fishery, largely foreign trawlers, takes fish from 500 to 600 mm FL. Intermediate-sized fish are conspicuously absent in both fisheries. Mid-sized fish are sporadically caught (Blunt 1969) but have never been observed in numbers to support the hypothesis that the small inshore fish grow and eventually join larger fish offshore. The difference in length could be due to disparate fishing methods but may also indicate inshore-offshore populations with different growth patterns. To better understand the growth potential of the inshore mackerel, I held a school in captivity for two years to observe growth. Some adjunct observations on maturation and the accumulation of energy reserves during captivity were also made, since these aspects of mackerel biology are still inadequately known. This report presents the results of these observations and compares them with observations made on fish in the wild.

METHODS

The observations on jack mackerel growth were made at the National Marine Fisheries Service, Southwest Fisheries Center in La Jolla, California. The fish were held in an outdoor circular swimming pool 7.3 m in diameter with 1 m of water (42 m^3 water volume). The pool had a fresh seawater inflow of 25 liters per minute and a recirculating pump with a capacity of 250 liters per minute. An overhead canopy shielded the pool from direct sunlight to reduce solar heating. The temperature ranged from 14.0° to 22.5°C and averaged 17.8° during the 2-year period. The fish were purchased from a bait dealer who caught them with a purse seine approximately 5 km southwest of La Jolla. The fish were fed daily until satiation with either chopped anchovy or squid and occasionally frozen euphausiids. The fish, about 200 in number, were feeding well and appeared adapted to captive conditions by the end of two weeks, when observations began.

I observed growth by sampling the school at various elapsed times and noting the change in fork length. The number of fish sacrificed and the elapsed times from the beginning were:

[Manuscript received March 22, 1984.]

Elapsed time in days	0	62	121	180	240	322	411	505	600	733
Number of fish sacrificed	24	22	20	10	10	10	11	10	11	23

No fish were added or replaced after removal of samples. Routine data on individual fish included fork length (FL) to the nearest 1 mm, body weight to the nearest g, sex, and gonad weight to the nearest g. I calculated the gonosomatic index—gonad weight/body weight x 100—for all fish. Observations were terminated after two years because some of the fish appeared to be in declining health and were not feeding well, possibly because of long-term stress.

The von Bertalanffy growth equation,

$$l_t = L_\infty [1 - e^{-k(t - t_0)}]$$

where

l_t = fork length at time t in mm,
L_∞ = maximum expected fork length,
t_0 = hypothetical time of zero length,
t = elapsed time in years after start of experiment,
k = a constant pertaining to metabolism

was applied to the length-time data to describe the growth and estimate L_∞, the length the fish would have reached had they remained indefinitely under laboratory conditions. I used a computer program (Abramson 1971) utilizing the least squares procedure of Tomlinson and Abramson (1961) to estimate the parameters.

The weight-length relation was determined by fitting the weight-length data to the equation $W = aL^b$

where

W = weight in g,
L = fork length in mm,
a = a constant,
b = slope of line after log transformation.

After growth observations, I measured the fat and water content in the red muscle, white muscle, viscera, and body as a whole of some of the laboratory fish and also of some sea-caught fish. The sea-caught fish were captured by a Russian trawler about 250 km from the California coast and were frozen. I used five fish from each group for whole-fish fat analysis. Each fish was passed through a meat grinder several times for homogenization and dried to constant weight at 55°C in a vacuum oven. Fat extraction was accomplished with a Soxhlet apparatus using chloroform and methanol as suggested by Kvaric and Muzinic (1950). Prior to homogenization, I measured the cross-sectional areas of the fishes' red and white muscle bundles. The measurements were made from a transverse steak taken one-third of the fish length anterior to the tail, as suggested by Greer-Walker and Pull (1975). I traced the outlines of the muscle areas onto a sheet of clear plastic and measured them with a planimeter.

Seven laboratory and seven wild fish were used for red muscle, white muscle, and visceral fat analysis. I dissected the red and white muscle tissues from the musculature at mid-fork length near and above the lateral line. The viscera included all the organs in the body cavity except the kidneys, which were inadvertently excluded. The procedure for fat analysis was the same as for whole fish.

RESULTS

The distribution of fish lengths at the various elapsed times and the von Bertalanffy growth curves for the captive and wild fish are given in Figure 1. The parameters describing the growth of the captive and wild fish are presented in Table 1. Figure 1 shows the two curves beginning at a time when the captive and wild fish were 243 mm FL, ($t = 0$; equivalent age is 2.26 years for wild fish). The curves show that an average fish in the laboratory grew to 408 mm FL for an increase of 165 mm during the 2-year period, while a typical wild fish would have grown to 304 mm FL for an increase of only 61 mm. Calculations with the Wine-Knaggs equation indicate that the time required to grow from 243 to 408 mm FL is 6.55 years. Hence the captive fish put on more than 6 years of growth in 2 years.

The estimate of L_∞ (Table 1) for captive fish suggests that they could have grown to an average fork length of 463.9 mm had they remained indefinitely under laboratory conditions. The L_∞ value for captive fish is much lower than that for wild fish (602.9 mm FL), although the captive fish had a higher growth rate during the 2 years under observation. Mackerel in the sea attain lengths slightly over 600 mm FL (MacCall and Stauffer 1983) and live over 30 years (Fitch 1956). The relatively high K value for captive fish indicates that their growth rate was declining rapidly. The t_0 values are not directly comparable because of differences in computation.

Many of the captive fish grew significantly larger than fish taken in the inshore southern California

TABLE 1
Estimated Growth Parameters in the von Bertalanffy Equation for Captive and Wild Jack Mackerel

	L_∞ (mm FL)	K	t_0 (years)
Captive fish	463.9	0.6836	−1.08
S.E.	16.1	0.0919	0.10
Wild fish	602.9	0.0935	−3.25
(Wine and Knaggs 1975)			
S.E.	5.9	0.0027	0.11

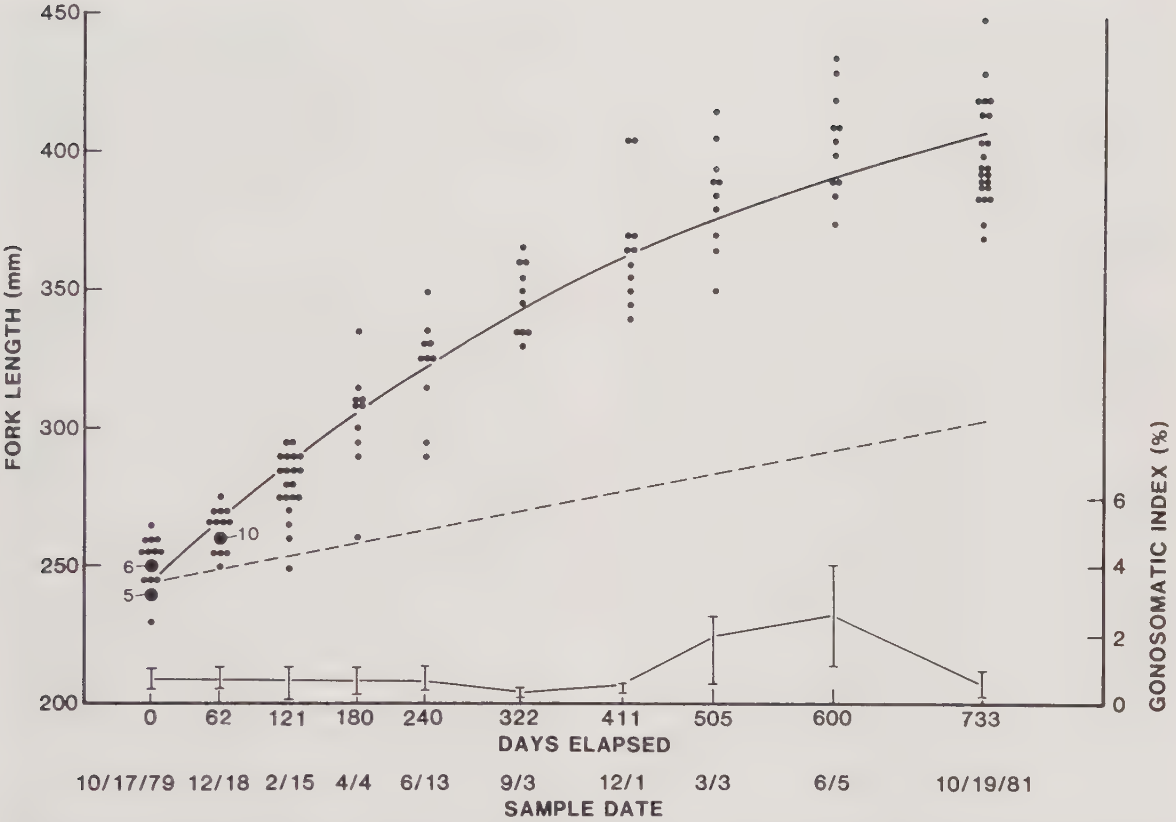

Figure 1. Growth of jack mackerel in the laboratory compared to growth of mackerel in the sea, and female ovarian development during captivity. Upper scale shows the distribution of fork lengths at elapsed times, the growth curve for fish in the laboratory (solid line), and the growth curve for fish in the sea (dashed line). Lower scale gives the ranges and means of female gonosomatic indices at sampling dates.

fishery. Data from Mallicoate and Parrish (1981) reveal that only a few mackerel of more than 20,000 sampled were over 350 mm FL, and none were over 380 mm FL during the years 1966-70. Most of the laboratory fish were larger than 350 mm FL in the 411-day sample (Figure 1), and none were less than 350 mm FL in the last three samples. The largest captive fish sampled was 450 mm FL. The sample of offshore fish in the present study contained 24 of 100 fish measuring less than 450 mm FL, with the two smallest between 300-350 mm FL. The remaining fish were larger, and two of the fish were over 600 mm FL.

The parameters describing the weight-length relationship for captive and wild fish are given in Table 2. The Wine and Knaggs equation is applicable to fish measuring 100-300 mm FL, according to MacCall et al. (1980), whereas their equation is more applicable to the entire range of lengths.

The weights (g) for some selected lengths calculated from these equations are:

Length (mm FL)	250	300	350	400	450
MacCall et al. (1980)	171	294	465	692	982
Wine and Knaggs (1975)	177	319	524	807	1179
Captive fish this study	179	356	635	1048	1632

The calculated weight, 179 g, for the captive fish at 250 mm FL is not very different from the values obtained with the other equations. This difference increases markedly with length, however, and captive fish of 450 mm FL would weigh nearly 1.4 times as much as wild fish of similar length from the Wine-Knaggs equation and over 1.6 times as much as fish from the other equation. Calculations with the weight-

TABLE 2

Estimated Parameters in the Weight-Length Equation, $W = aL^b$, for Captive and Wild Jack Mackerel

	a	*b*
Wild fish (Wine and Knaggs 1975)	0.0000033101	3.223229
Wild fish (MacCall et al. 1980)	0.000012338	2.97785
Captive fish this study	0.000000176	3.75670

length equation for captive fish indicate that the weight should have increased from 161 to 1130 g as the mean length increased from 243 to 408 mm FL during the 2-year holding period. Calculations with the Wine-Knaggs length-growth equation and the weight-length equation from MacCall et al. (1980) indicate that mackerel in the sea would require 10.8 years to grow from 161 g to 1130 g. It thus appears that the captive fish gained weight about five times faster than fish in the wild.

The average whole laboratory fish contained less water (50.2% vs 70.7%) but more fat per unit wet weight (25.7% vs 6.4%) than the average sea-caught fish (Table 3A). The values for the sea-caught fish were close to those found for *Trachurus trachurus*, which had an estimated moisture content of 76.7% and fat content of 6.8% (Sidwell et al. 1974). The average laboratory fish used in whole-fish fat analysis was slightly longer—433 vs 426 mm—but much heavier—1332 vs 850 g—than the average sea-caught fish. For a further comparison of the wet and component weights, I calculated the expected wet weight of a 430 mm FL fish from the weight-length relationship for both groups. I then estimated the water, fat, and fat-free dry weights with the percentages in Table 3A. The calculations (Table 3B) show that fat accounted for 65.2% of the difference in wet fish weight, water only 8.4%, and fat-free dry weight 26.4%. The large difference in fat-free dry weight is of particular interest because it implies that the laboratory fish stored a substantial amount of protein in addition to fat.

The red muscle, white muscle, and viscera of the laboratory fish all contained much more fat per unit wet weight than did the sea-caught fish (Table 4). The viscera and white muscle of the laboratory fish had about 7.1 and 8.6 times more fat per unit wet weight than those of sea-caught fish. The percentage of fat in the red muscle of the laboratory fish was only 4.5 times higher, suggesting that the increase in fat was not distributed proportionately to the three body areas. The viscera were highest in fat content, followed by red muscle and white muscle in captive as well as sea-caught fish. Although lower in relative fat content, the white muscle tissues probably contain more total fat because they occupy a much greater portion of the body volume. The water content was higher in sea-caught fish for the three types of tissues examined.

The red and white muscle bundles appeared to have enlarged proportionately with fish girth, because the percentage of red muscle to total muscle was nearly the same at 11.1% and 10.8% (Table 3). These percentages were much lower than the 18.3% recorded for *Trachurus trachurus* by Greer-Walker and Pull (1975). Much of the difference may be due to technique and the exact position of the transverse cut. The same technique was applied to both laboratory and sea-caught groups of jack mackerel.

The ovaries of the captive females were most highly developed during June 1981 (Figure 1). The eggs in the more mature ovaries were heavily yolked, and measured 0.5-0.7 mm in diameter, about the maximum size found by MacGregor (1966 and 1976) in his fecundity studies. Ichthyoplankton surveys indicate that June is one of the peak spawning months (Ahlstrom 1956; Farris 1961). The gonosomatic indices for the males were all under 1% except in June 1981 when two of the five males sampled had indices above 2%.

TABLE 3

A. Comparison of Water, Fat, Red Muscle, and Size of Five Laboratory and Five Sea-Caught Mackerel

	Laboratory		Sea-caught	
	Mean	S.E.	Mean	S.E.
Percent water[a]	50.2	1.4	70.7	1.4
Percent fat[a]	25.7	3.9	6.4	1.7
Percent red muscle to total muscle[b]	11.1	0.5	10.8	0.5
Fork length mm	443	4.8	426	4.5
Wet weight g	1332	49	850	46

B. Comparison of Wet and Component Weights (g) of Laboratory and Sea-Caught Fish[c], Applying above Data

	Laboratory	Sea-caught	Difference	Percent of 428-g wet weight difference
Weight of Water	655	619	36	8.4
Weight of fat	335	56	279	65.2
Fat-free dry weight	314	201	113	26.4
Wet weight of 430-mm mackerel[d]	1304	876	428	100.0

[a] Percent based on wet weight.

[b] Percent red muscle measured from transverse cut.

[c] Standardized to 430 mm.

[d] Wet weight obtained from weight-length relationship within each sample.

TABLE 4

Comparison of Seven Laboratory and Seven Sea-Caught Mackerel

	Laboratory		Sea-caught	
	Mean	S.E.	Mean	S.E.
Red muscle				
Percent water	48.4	1.7	71.2	0.8
Percent fat[a]	31.9	2.5	7.1	1.1
White muscle				
Percent water	63.5	1.9	75.0	0.8
Percent fat	12.7	1.9	1.5	0.3
Viscera				
Percent water	25.4	2.6	75.2	1.4
Percent fat	67.5	9.1	9.6	1.5
Length (mm)	394	3.0	395	16.2
Weight (g)	907	55	593	85

[a] Percent water based on wet weight.

These two males produced sperm upon stripping and appeared capable of spawning. The water in the tank was checked regularly for eggs but no sign of actual spawning was detected. The females did not show signs of advanced ovarian development during June of 1980, although they were large enough to be sexually mature (235 mm FL) according to Wine and Knaggs (1975).

DISCUSSION

The abundant food supply and lack of predators undoubtedly contributed much to the high growth rate observed in this study. The temperature and the absence of spawning may also have been important in increasing growth. The large increase in growth by fish in the laboratory over fish in the sea has been observed for other pelagic species including the Japanese jack mackerel, *Trachurus japonicus* (Ochiai et al. 1983) and northern anchovy, *Engraulis mordax* (Hunter and Leong 1981). In spite of the rapid growth rate observed, the ultimate length, L_∞, attainable by the captive fish appeared to be relatively small. The stress of confinement in a small volume of water and missing elements in the diet over an extended period are factors that can limit growth.

The captive fishes' growth in length exceeded that of the wild population by about three times. The captives' greater growth in body weight—about five times—suggests that the food ration exceeded that needed for skeletal growth and that growth in length may have been near the maximum for the given conditions. It is not surprising that a large food supply increased fat deposition, but the finding that it also resulted in a substantial increase in fat-free dry weight suggests that excess rations are stored not only as fat but also as protein.

That fact that some of the captive fish grew beyond 425 mm FL and one reached 450 mm FL indicates that the small jack mackerel in the inshore regions off southern California have the potential to reach those lengths. Observations in the present study do not exclude the possibility that these inshore fish have the potential to grow even larger.

ACKNOWLEDGMENT

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MEASURING PHYSICAL-OCEANOGRAPHIC FEATURES RELEVANT TO THE MIGRATION OF FISHES

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ABSTRACT

Knowledge of the physical marine environment is a prerequisite to understanding migration of fishes. Variations in currents, drifts, tides, upwelling and other forms of motion in the ocean have direct and indirect effects upon the timing and paths of migration and upon reproductive strategies in general. This paper reviews some of the approaches for studying the marine environment that should be considered in developing projects concerning the migration and distribution of fish stocks. The three principal sources of physical oceanographic data are 1) publications and archives, 2) agency monitoring programs, and 3) field measurements. Physical data taken contemporaneously with fish observations have particular value. All three sources are frequently combined in a well-planned project. Remote sensing of the marine environment is an important new method that is now being used to influence the deployment of research and industry vessels.

INTRODUCTION

An important factor in the migration of fishes is the fields of motion in the ocean environment. Water motion, as it may influence fish stocks, occurs across a broad range of temporal and spatial scales. It can impinge directly upon fish in the form of long-term drift or strong, short-term advection by currents or tidal flow. It also can act in an indirect manner by creating or destroying food aggregations. Upward motion enriches the euphotic zone. Olfactory clues for migrating fish may be carried with the flow, and proper spawning habitats may depend on flow patterns. Fish may move with the drift or swim against it. These fields of motion may be used selectively by fish. Current systems often undergo cyclical changes in response to tidal or seasonal events, and they usually show even larger aperiodic fluctuations.

The published literature contains some excellent studies in which some part of the cycle of fish migration is associated with water motion or other events in the physical environment. There are other studies, however, which appear to have been handicapped by a failure in their design to give adequate attention to the vagaries of the ocean. There is a definite need to take physical-oceanographic measurements that might assist in explaining observed biological phenomena. The objective of this presentation is to review some approaches for studying the physical environment that should be considered in developing projects concerning the migration or distribution of fish stocks. It is not my intent to outline complex and expensive research into physical oceanography, but rather to consider some relevant measurements of the ocean that are affordable by a migration research group with a modest budget and which might indicate some physical order to biological distributions and might cue or direct migratory behavior.

EDDIES AND OCEAN FRONTS

Two major features in the ocean that form strong patterns in the distributions of physical characteristics are fronts and eddies. Fronts and eddies are regions where ocean dynamics are intensified. They are regions of horizontal shear, convergence and divergence, and vertical convection. Owen (1981), in a review of these classes of motion and their biological consequences, noted that diverse marine life forms, from the very small to the very large, alter their distributions in the presence of such flow patterns.

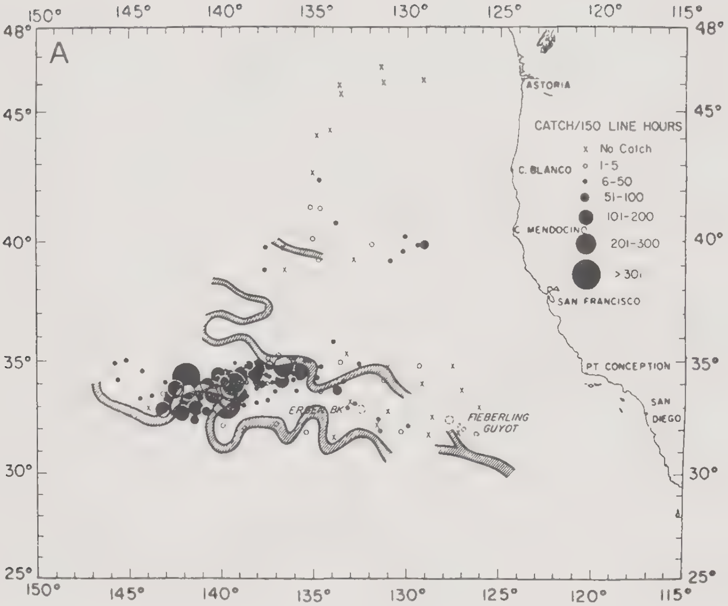
Eddies may be classified as free or stationary. Free eddies are formed from flow instabilities and atmospheric forcing. Examples include the warm-core and cold-core eddies that are formed when meanders are pinched off major current systems such as the Gulf Stream and the Kuroshio. These eddy "rings" transport large amounts of heat, salt and biota. The effect of such an eddy is the injection of a community of organisms and a body of water into a foreign water mass. However, free eddies are unlikely to provide a reliable mechanism for fish migration because of their episodic nature.

Stationary eddies, on the other hand, are topographically controlled and therefore persistent. Their circulation patterns are determined by banks, islands and the configuration of coastlines. They usually are semipermanent features but may have a large range of fluctuation. The Southern California Eddy (reviewed by Owen 1980) is an example of a stationary cyclonic eddy in which vertical convection produces an upward transfer of nutrients into the euphotic zone. A large number of studies has shown the Southern California Eddy to be a refuge for a variety of organisms including pelagic fishes. Smith (1978) found that the region about the Southern California Eddy, which comprises only 12% of the spawning area of the northern anchovy's (*Engraulis mordax*) central subpopulation, contained, on average over 24 years, 48% of the spawned larvae.

Ocean fronts may be classified into five major categories. Fronts are formed 1) at the boundary of intense currents, 2) in regions of convergent surface flow driven by wind stress, 3) as a result of coastal upwelling, 4) at boundaries of estuarine discharge plumes, and 5) as a result of restratification of water from tidal or wind stirring in regions of shallow topography. In the major oceans large-scale fronts lie in zonal bands in response to the time-integrated effect of large-scale wind stress.

Well-studied examples of ocean fronts are the subarctic and subtropic fronts of the North Pacific Ocean. The subarctic front lies about the 40°N parallel, except near its eastern terminus, where it curves southward to the vicinity of 35°N. The subtropic front lies near the 32°N parallel. In the 1970's the distribution of albacore (*Thunnus alalunga*) as they migrated toward the North American summer troll fishery was investigated in relation to these fronts (Laurs and Lynn 1977). In the late spring of 1972 and 1973 the fronts were well developed. The fronts had spatial continuity and strong gradients of temperature and salinity. Albacore catches were distributed along and between the fronts (Fig. 1). Such aggregation may have occurred in response to the availability of forage. The forage, in turn, was dependent on lower trophic levels and ultimately on the high productivity created by frontal dynamics. The changing patterns in the size composition of the albacore in these offshore catches over 7 weeks were repeated, after a delay, in the nearshore fishery, indicating that albacore were actively migrating through this area during the period of the study.

A repeat of the survey in the late spring of 1974 revealed significant differences (Fig. 1). The frontal structure was poorly developed and water-mass boundaries were less distinct. Albacore catches were made over a larger region and did not tend to persist in any local area as they had in the previous 2 years. There was, however, one pocket of high catches that was sustained over several days. A frontal meander of modest proportions nearly encompassed these catches. A sequence of catches--first within the meander, then coastward of the meander, followed by a recurrence of catches within the meander--suggested a funneling of the migrating albacore related to the feature. Thus, spring distribution and migration of albacore seem strongly influenced, whether directly or indirectly, by the presence of these large-scale fronts, the degree of development of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ASTORIA
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x No Catch
1-5
6-50
51-100
101-200
201-300
>301
C. BLANCO
C. MENDOCINO
SAN FRANCISCO
PT CONCEPTION
SAN DIEGO
ERBEN BK
FIEBERLING GUYOT

Figure 1. Albacore catch per 150 line-hours by 12 chartered fishing vessels during a preseason exploratory study and the subarctic (northern) and subtropic (southern) ocean fronts during (A) 1973 and (B) 1974 (from Laurs and Lynn 1977).

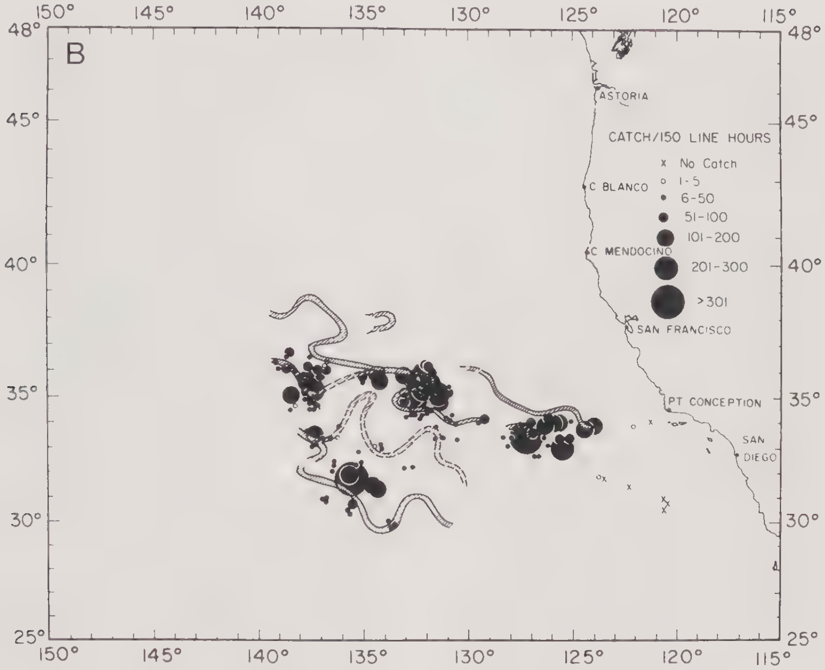
the fronts and the form of mesoscale features within the fronts.

OTHER CLASSES OF MOTION

Classes of motion which impact biological distributions, other than fronts and eddies, include coastal upwelling, current systems, long-term drift, turbulent mixing, tides, and river flow. In a comparative study of oceanographic regimes and spawning strategies within the California Current system, Parrish et al. (1981) described the seasonal cycle of upwelling, offshore transport and nearshore countercurrents. The reproductive strategies of pelagic fish in this highly productive region were shown to accommodate to these seasonal fluctuations in nearshore coastal dynamics. The strategies include seasonal timing, short planktonic stages and large numbers of spawn.

CONVENTIONAL OCEAN MEASUREMENTS

Methods of ocean measurement must be chosen with consideration for the characteristics of the species of fish studied as well as the availability of financial and manpower resources. The objective of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1-5
6-50
51-100
101-200
201-300
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C BLANCO
C MENDOCINO
SAN FRANCISCO
PT CONCEPTION
SAN DIEGO

Figure 1 continued.

such measurements of ocean currents is to estimate the effective fields of motion over spatial and temporal time scales that are pertinent to the migrations of a particular population of fish. Often there is no obvious method to achieve the desired results directly. Moored current meters can provide relatively dense coverage in time. However, if one is to achieve reasonable coherence among current meters, a modest deployment can cover only a small part of the migratory domain. That still might represent a large investment in time, effort and money. Thus current meters are most effective in confined regions such as channels, embayments and continental shelves. In the open ocean current meters usually involve logistics of such proportions that they would dominate, in an operational sense, a modest project on fish migration.

Other direct methods of current measurement used in larger-scale regions are drogued drifters, ship's drift and, in coastal zones, drift cards. Recently, acoustic doppler logs and expendable temperature/velocity probes have been used successfully to measure velocity profiles from a moving vessel.

More commonly, we observe fields of motion indirectly by sampling the density (temperature and salinity) field in hydrographic Conductivity/Temperature/Depth (CTD) surveys from which geostrophic velocities can be computed and water masses and fronts located. Other variables such as water clarity, productivity and oxygen content can also be measured. Distributions of these variables may strongly influence the distribution and movement of fish. This method has limitations which arise from the assumption of synopticity, and it produces only one slice in time of a varying state. Repeated surveys (a costly endeavor), which are often done on monthly intervals, can be seriously biased. When data are too sparse to examine events within a season, an accumulation of measurements may permit calculation of long-term mean seasonal changes that may relate to mean seasonal distributions of fish. Other indirect methods include using Ekman drift to estimate time-varying aspects of surface currents over periods of weeks to months and using records of tide level to follow changes in coastal currents.

Sources of Ocean Data

The sources of data for marine environmental studies may be divided into three principal categories.

1. One source is historical files in the form of data archives, scientific literature, and summary publications including atlases.

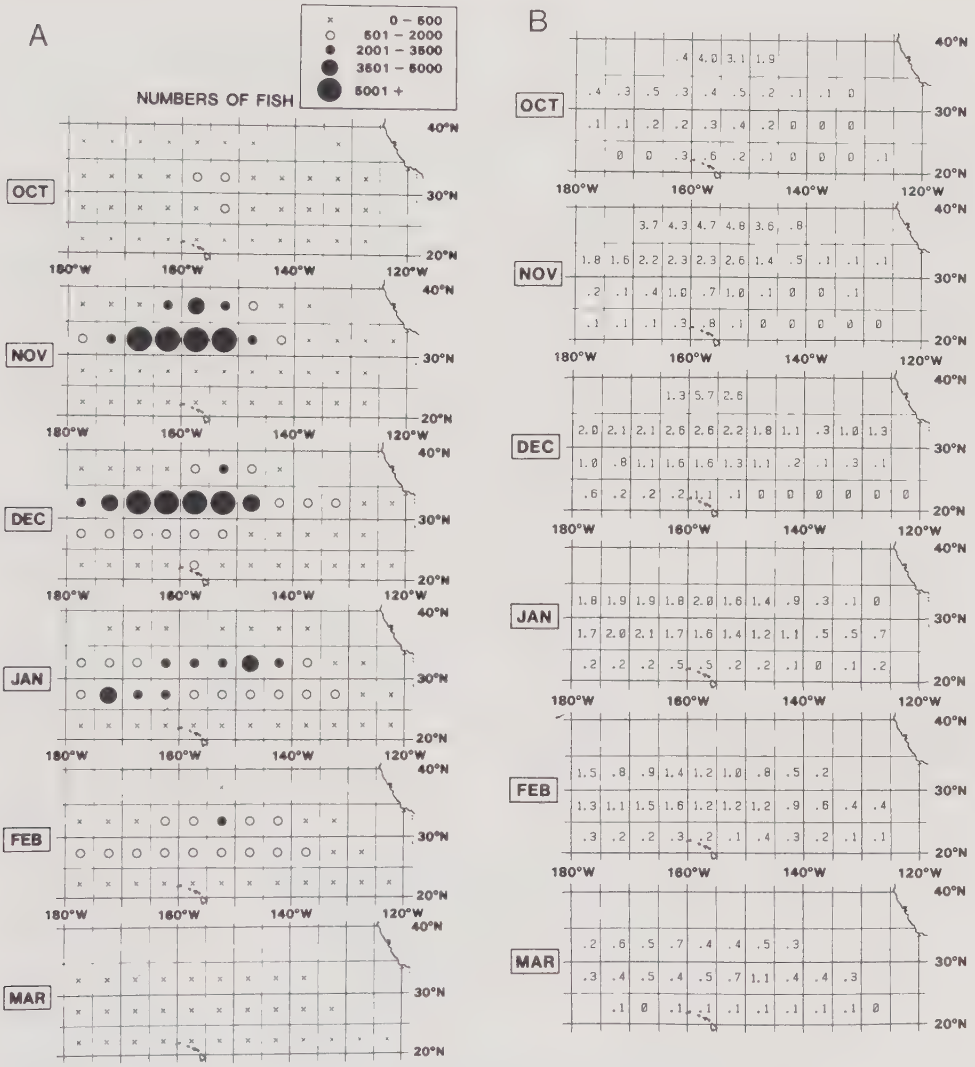
2. A second source is ongoing ocean monitoring programs. These programs, often found in government agencies and universities, may provide ocean data in the planning stages or during the operations of a study project. Examples include maritime reports of weather and sea-surface temperature, remote-sensed satellite imagery, and sea level.

3. The third major source is field measurements conducted during fisheries studies. These data have particular value in being contemporaneous with observations of fish. They may come from measurements aboard a research vessel or gathered by arrangements aboard commercial fishing vessels or other ships-of-opportunity.

Perhaps a fourth source is model simulations of ocean dynamics. Most or all of these sources usually are brought to bear upon a problem.

Case Studies

For example, let us look at a project in progress involving albacore tuna; it uses all three principal data sources. A phase of the complex migration of North Pacific albacore is the movement following the seasonal decline of the United States-Canadian surface fishery in the fall to the subsurface longline fishery conducted in winter by Japan, South Korea and Taiwan. This is a southward and westward movement from a region offshore of the US west coast to a broad zone across much of the North Pacific. Catch records of the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160°W
140°W
120°W
40°N
30°N
20°N

Figure 2. (A) Japanese longline albacore catches in the eastern north Pacific for October through March averaged for 1969-1979 (from Lynn and Bliss 1982). (B) The same data as catch per 100 hooks.

Japanese longline fishery for albacore east of the international dateline (Lynn and Bliss 1982) show that the major catches in the eastern North Pacific are taken between 30°N and 35°N during the months of November through February (Fig. 2a). In the early part of this period there are also some modest catches north of 35°N and between 145°W and 165°W. The interesting aspect is that the catch rates north of 35°N are high (Fig. 2b). Based upon a resolution of monthly catch totals for 5° blocks of latitude and longitude, the catch rates are close to five albacore per 100 hooks compared to no more than two to three per 100 hooks elsewhere. We know from earlier work that the subarctic front lies within the zone of 35°N to 40°N. November is a period of cooling and deepening of the shallow, seasonal, mixed layer. Beneath this layer there is the deeper frontal structure remaining from the previous winter. Oceanographic atlases (e.g. Robinson 1976) show that in November the 16 C to 18 C isotherms from the surface to 60 m fall in this zone (Fig. 3) and are thus coincident with the mean position of the subarctic front. This range of ocean temperature is characteristic of albacore fisheries. These conditions suggest that in the early phases of the longline fishery, as albacore and surface layer isotherms retreat from northerly latitudes, the albacore are once again aggregated by events about the subarctic front, thus producing the circumstances that result in high catch rates. By mid or late December temperatures about the front are lower than those apparently preferred by albacore and catches decrease accordingly.

This background information influenced the strategy developed for recent exploratory longline surveys (Laurs et al. 1981, 1982). In these surveys US fishing vessels experimented with gear and methods in a project conducted by the American Fishermen's Research Foundation and carried out in cooperation with the National Marine Fisheries Service, under the scientific leadership of R.M. Laurs. Five fishing vessels are participating in the recent survey. Prior

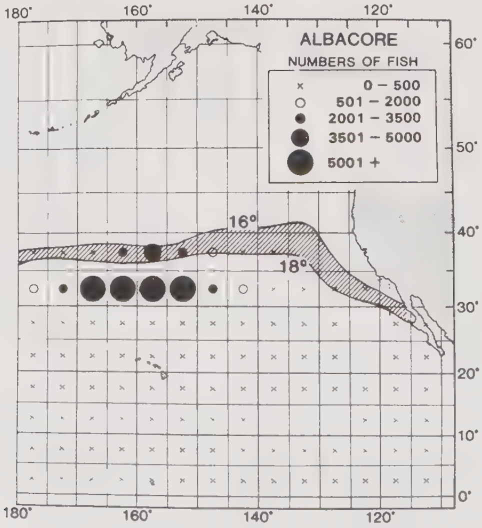

Figure 3. The albacore longline catch for November from Figure 2A and the monthly mean 16 C and 18 C isotherms.

to sailing, up-to-date expendable bathythermograph (XBT) data were obtained from the US Navy's Fleet Numerical Oceanographic Center. Plots of isotherm depth in the upper 150 m of the survey region revealed a zone of abrupt changes identifying a strong front. Thus, an ocean monitoring program provided input for tactics in deploying the vessels. Each of the five vessels was instructed to record twice-daily weather and sea conditions and sea-surface temperature. Also, each vessel made daily XBT casts. This measure of thermal structure, taken concurrently with fishing operations, will be combined with the background information to address the question of the association of migration with ocean fronts.

The 1972-74 albacore surveys (Laurs and Lynn 1977) in which the spring migration into the North American surface fishery was investigated, offer an example of a more comprehensible level of operations using physical oceanography in conjunction with fisheries research. The surveys combined the use of the R/V DAVID STARR JORDAN and chartered commercial-fishing vessels. The JORDAN conducted oceanographic observations on a planned grid. Traditional observations were made: CTD profiles; XBT and water bottle casts; continuous recording of surface temperature, salinity and chlorophyll concentration; and analysis of water bottle samples for O_2 and chlorophyll concentrations. Nutrient chemistry was desired but proved to be beyond our resources. Micronekton tows, to obtain potential forage organisms for albacore, were made using an Isaacs-Kidd midwater trawl. The JORDAN also trolled for albacore as time permitted. The catches made by the JORDAN, while not comparable in effort to those of the chartered fishing vessels, did provide confirmation that areas well beyond the regions of fronts were less productive or unproductive. The chartered fishing vessels recorded weather and sea conditions and made XBT casts. These additional physical observations extended our interpretation of the ocean conditions beyond the grid covered by the JORDAN.

An added factor in these surveys was the cooperation of unchartered fishing vessels. Daily broadcasts of findings from the JORDAN and chartered fishing vessels were given on radio frequencies used by fishermen. Many of the fishermen responded in kind by reporting their daily catches, thus assisting in the success of the operations, and many also voluntarily completed catch logs as part of an interstate and federal program (Laurs et al. 1975). This project combined a number of activities directed toward describing and understanding the migration of albacore of which the study of the physical environment was an integral part.

Interpreting and Using Ocean Measurements

The CTD, XBT and water-sample casts provide the basis for identifying water masses and fronts (Fig. 4) and for calculating the dynamics of stability, mixing and geostrophic currents. Meanders or

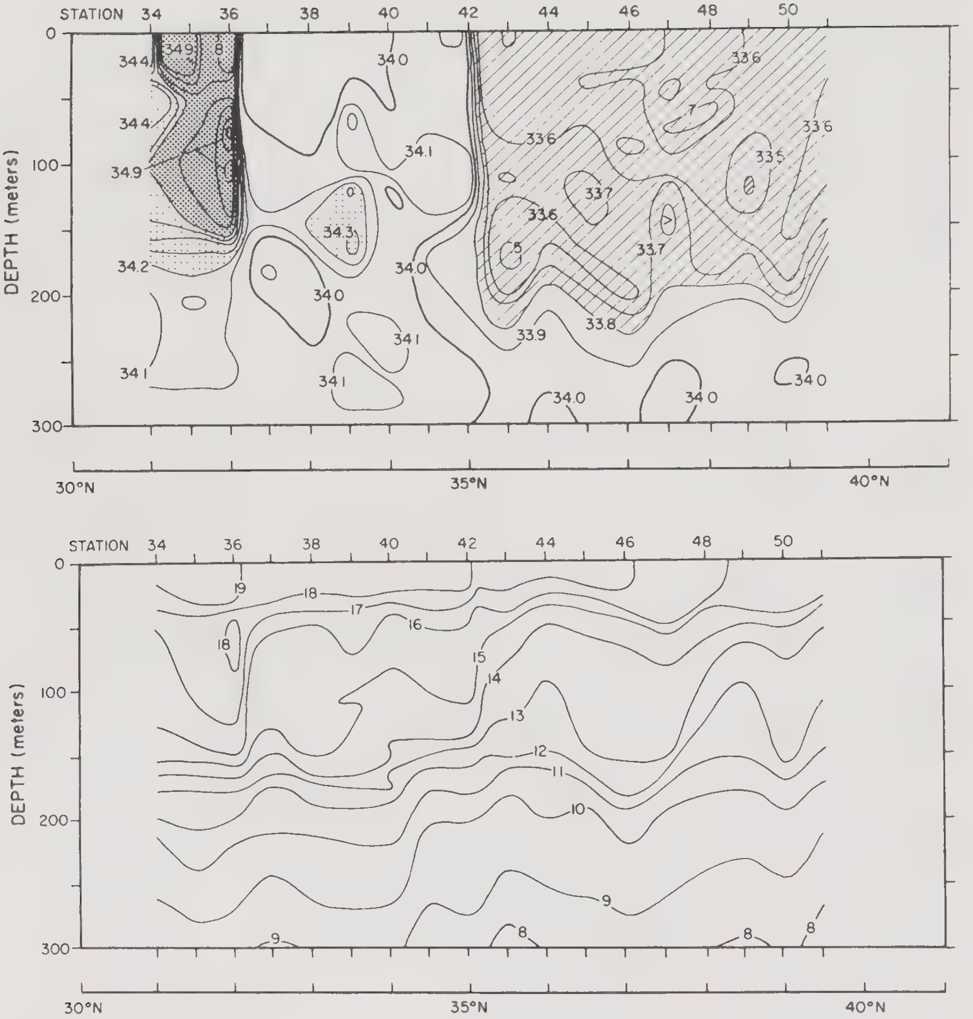

Figure 4. Vertical section of salinity (upper panel) and temperature (lower panel) along 137.5°W for June 1973. The subtropic front is seen at 32°N and the subarctic at 35°N. Hatching indicates salinities < 33.8 °/oo; light stippling indicates salinities between 34.2 and 34.6 °/oo and heavy stippling indicates salinities > 34.6 °/oo.

eddies spun off the fronts can be described. The nutrient chemistry, chlorophyll determinations and micronekton hauls provide the links between the physical and biological regimes. The thermosalinograph, which provides a continuous underway recording of surface layer temperature and salinity, reveals the presence of surface frontal gradients as they are crossed (Fig. 5). Thus, opportunity arises for

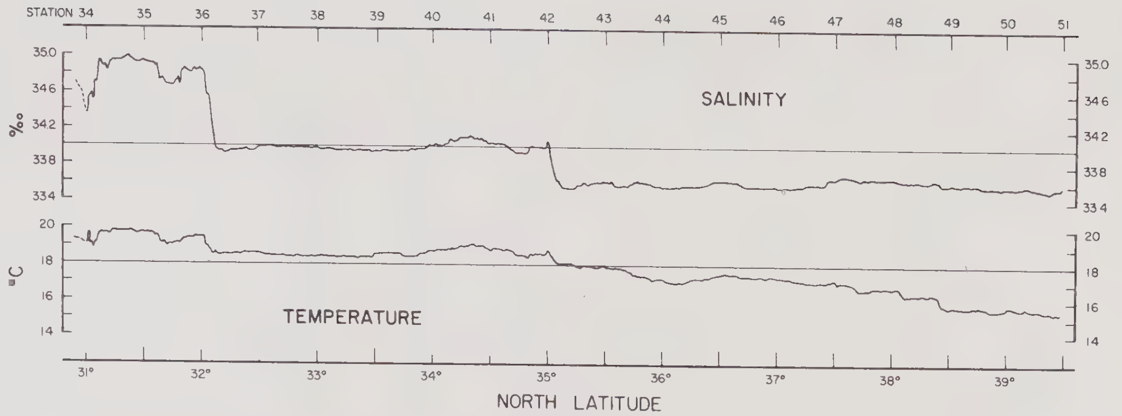

Figure 5. Surface temperature and salinity recorded by thermosalinograph along the same track as in Figure 4.

a tactical response in sampling procedures and fishing operations. The temperate zone frontal system of the eastern North Pacific Ocean often exhibits a temperature change on the order of only 0.7-1.0 C in 4-20 km. It is the abruptness of change in an otherwise flat signal that identifies these features. The salinity change at the front, 0.5-1.0 ^{o}/oo, is even greater relative to its ambient fluctuations in the surface layer.

APPLICATIONS OF REMOTE SENSING

Remotely sensed measurements from aircraft and satellites have been employed in directing commercial-fisheries and fisheries-research operations and in analysis of the results of biological- and physical-oceanographic projects. This powerful tool is growing in acceptance and importance in the fishery sciences and industries. The applications of satellite remote sensing in fisheries, including the use of thermal infrared radiometry, the Coastal Zone Color Scanner (CZCS), and the SEASAT-A microwave scatterometer, has recently been reviewed by Laurs and Brucks (in press).

For many ocean scientists the initial exposure a decade ago to thermal-infrared images from satellites raised questions as to relevance of the images to subsurface features. Experience has demonstrated that, for the most part, the observed plumes, fronts, eddies, wakes and the like are features rooted in the mixed layer or deeper. In a time sequence of satellite images some are found to evolve slowly in form; others show a strong response to major wind events in a short time. This imagery reveals expressions of the advection and exchange processes at the surface and potentially reflects related patterns in the biological distributions.

The major, western, boundary-current systems are monitored by satellite. Contemporary multidisciplinary studies of the warm- and cold-core rings in the North Atlantic rely upon remotely sensed data. Satellite imagery is equally useful in small-scale studies and in the lesser-gradient features found in eastern boundary currents. Using images from the NOAA-5 satellite, Simpson and Pingree (1978) confirmed the occurrence of convergent tidal fronts in the Celtic Sea. These shallow sea fronts divide regions of tidally mixed and well-stratified waters. They stimulate local primary productivity and concentrate zooplankton. At the National Marine Fisheries Service Southwest Fisheries Center (NMFS/SWFC) we have used imagery to direct effort in a detailed survey of an upwelling plume. Also the SWFC participated in a joint venture of industry, university and government to supply salmon and albacore fishermen on the US west coast with timely maps of gradient features (Montgomery 1981). Recently the development of processing techniques for data from the CZCS aboard the Nimbus 7 has added a new instrument to our arsenal. R.M. Laurs and colleagues are studying an application of the CZCS to the west coast albacore fishery, which has altered our perception as to the mechanism of response of these fish to upwelling fronts. Albacore, which are visual feeders, are now suspected to be responding to strong changes in turbidity which are seen as color fronts associated with upwelled waters rather than to the temperature fronts (R.M. Laurs personal communication).

R. Lasker and colleagues at the SWFC are applying satellite imagery to studies of northern anchovy spawning in the Southern California Bight. Anchovy eggs and larvae were sampled during March and April 1980 in a closely spaced grid of stations covering most of the Bight. The first-day larvae were well represented in net tows in some areas and absent from others. There was remarkable coincidence in the larval distribution's southern boundary with a strong gradient of chlorophyll concentration as measured by the blue-green ratio in a CZCS image taken in early April, 1980. Spawning appears to have occurred within the plankton-rich areas and was absent from the clear blue, and more sterile, waters offshore and to the south. The northern limit of egg distribution was coincident with the 14-C surface isotherm as determined by direct measurements and thermal IR satellite imagery. Temperatures less than 14 C, while not physiologically unsuitable for anchovy spawning, indicate recently upwelled waters. The 14-C isotherm may denote a zone of change in the succession of planktonic-community composition or in the vertical stratification of the water column, both of which are important factors in spawning (Lasker 1978). A repeated set of data for February 1981 did not confirm the correspondence with the surface-chlorophyll gradient. More observations are scheduled.

PRESENT DAY DEVELOPMENTS AND FUTURE EXPECTATIONS

I expect application of remote-sensing techniques to continue to advance our understanding of the oceans and to expand in usefulness in marine biology. There are several recent improvements in remote sensing, and more are anticipated. The present application of thermal IR imagery is to utilize the relative temperature-gradient patterns for interpretation of events. Until recently the accuracy of estimates of sea temperature from single channel IR data was no better than 4-5 C (or 2-3 C if sea surface measurements were available). Algorithms have now been developed for multichannel IR data, limiting error to 0.6-0.9 C (Bernstein 1982; McClain et al. 1983).

Overcast and atmospheric moisture continue to be the major problems in collecting useful IR and visual imagery. Bernstein (1982) has devised a routine which retrieves sea-surface temperatures even from small scattered openings in clouds. Using image-screening techniques the routine eliminates all but the best data. Applying the routine to a series of images collected over days to weeks produces a field of data not unlike that from maritime ship reports. The satellite data have a smaller bias than do maritime ship reports,, however, and are not constrained to shipping lanes. This routine might be used to improve the present program for monitoring sea-surface temperature that relies on maritime reports and would likely improve the spatial resolution. It also could be applied regionally.

One experimental sensor that is unaffected by clouds is the microwave scatterometer used aboard the ill-fated SEASAT-A. It provides the basis for estimates of wind stress. Bakun and Parrish (1980) have found a spatial alternation in the pattern of wind-curl stress along the California and Baja California coastal zone. A lobe of positive curl between regions of negative curl appears to block the seasonal development of the countercurrent, resulting in two semi-indepedent gyres. These gyres correspond to separate subpopulations of pelagic fish. The wind stress was derived from a composite of many years of data. The wind-stress curl could not have been resolved by the methods available for synoptic sampling. Bakun and Parrish suggested that the design resolution of 50 km for the microwave scatterometer would allow synoptic viewing of wind-stress features on a size scale relevant to fish stocks.

Within the past decade we have seen substantial technological advances in computers and in data handling systems. These improvements have facilitated the archiving and use of voluminous time series of environmental data. Numerous resulting studies and papers have examined interactions between the oceans and atmosphere on scales from regional to global. The benefits to fisheries research, which are yet to be fully realized, should include the development of environmental indices and simulation models which have potential for interfacing with fisheries data sets and migration models.

CONCLUSION

The linkage between the distribution and movement of fish and fields of motion and related ocean features is complex and involves multiple trophic levels. It may not be possible to demonstrate a direct causal relationship, but evidence and intuition point toward such linkages. Both physical and biological data sets tend to be deficient because the number of samples is usually small, the medium is highly variable, and most data sets require considerable interpolation. Despite these deficiencies, evidence is overwhelming for the influence of spatial and temporal variations in the marine environment upon fish. Hypotheses so raised can lead to improved experiments and alternate approaches to confirm or dispel the ideas.

The technological advances also provide for rapid data retrieval and sophisticated graphic display of data from oceanographic archives--quite the equivalent of an electronic atlas. As these developments become available they improve our capabilities for accessing marine environmental data for development of project plans and in analysis. However, the advances in remote sensing and data technologies do not supplant the need for field measurements but rather supplement them. There is still the need for lowering instruments over the side to take the measure of the ocean environment concurrently with sampling fish.

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Remotely Sensed Sea Surface Temperature Variability Off California During a "Santa Ana" Clearing

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During a prolonged clearing with particularly dry atmospheric conditions over the Southern California Bight, four NOAA 6 satellite overpasses at 12-hour intervals were recorded while a research vessel measured ocean temperatures within the field of view of the satellite. This data set is used to evaluate two versions of an equation for estimating sea surface temperature from satellite data and for examining short-term changes in surface temperature caused by diurnal variation and surface layer movement. Surface temperatures calculated from data taken during a daytime overpass, using two slightly differing versions of a multiwindow atmospheric correction equation, match the ocean temperatures within the expected range of scatter: ±0.6°C. One version has a mean daytime bias of +0.5°C, the other has -0.4°C, and thus the two versions differ by 0.9°C. The satellite-derived sea surface temperatures show a diurnal variation in the range of 0.25° to 1.0°C. Hence the bias of calculated satellite temperatures for the nighttime overpasses differ from those for the daytime; the bias in one version is +1.2°C and in the other is +0.4°C. It is suggested that these biases are caused by inherent problems in the selection and matching of satellite and ocean data sets used to determine the equation coefficients as well as poorly understood diurnal variation of the surface temperature as measured by satellite. Advection, evidenced by an image-to-image shift of thermal gradients over 12- and 24-hour periods can produce local temperature changes that add to the problem. Noise in one of the satellite data channels, another part of the problem, is shown to be amenable to filtering techniques. Diurnal differences in satellite-observed surface temperatures are found to vary regionally; larger variation is found in waters that are turbid and have a shallow thermocline. Near surface in situ temperature measurements suggest a diurnal layer variation of 0.2°C, much less than the variation observed by satellite. An estimation of diurnal sea surface temperature variation based on heat budget calculations supports the in situ observations.

INTRODUCTION

The accuracy of sea surface temperature estimation, using infrared (IR) radiometers aboard earth-orbiting spacecraft, is adversely affected by the attenuation of the atmosphere [*Maul and Sidran*, 1973]. The effect is principally due to varying amounts of water vapor and spatially unresolved clouds, which absorb and reradiate some of the IR radiation emitted from the ocean. As a result, radiometers measure lower brightness temperatures than they would under cloud-free and moisture-free conditions [*Barnett et al.*, 1979; *Bernstein*, 1982]. Differences of several degrees between radiometer-measured brightness temperatures and in situ sea surface temperatures (SST) are common. A small part of these differences is caused by the existence of a cool "skin" in the upper $10 \mu m$ which is sensed by the satellite radiometer and which is often 0.3°C to 0.6°C less than the in situ SST commonly measured at a depth of 1 m or so [*Paulson and Simpson*, 1981]. While several techniques have been developed to reduce the effects of atmospheric attenuation, it was only with the deployment of the Advanced Very High Resolution Radiometer (AVHRR) aboard the NOAA 6 and NOAA 7 polar-orbiting meteorological satellites that the means were provided to effectively accomplish it. The improvements in the AVHRR instrument over its predecessors include lower background noise in the data and the availability of multiple atmospheric-window channels in the IR bands.

Recently published algorithms that provide estimates of SST from IR brightness temperature [*Bernstein*, 1982; *McClain*, 1981; *McClain et al.*, 1983] utilize the advanced capabilities of the AVHRR. The algorithms provide for the selection of cloud-free data and the calculation of SST by using IR readings from two or three different spectral channels. The root mean square disagreement between calculated satellite SST and in situ ocean measurements has been shown to be 0.7°C or less. On the NOAA 6 the AVHRR has channels in the visible ;(0.6 - 0.7 μm), near IR (0.7 - 1.1 μm) and thermal IR (3.5 - 3.9 and 10.5 - 11.5 μm). These are referred to as channels 1, 2, 3, and 4, respectively. An additional channel (11.5 - 12.5 μm), referred to as channel 5, is available on NOAA 7. NOAA 8, launched on March 28, 1983, has the same configuration as NOAA 6.

During a 2-day period in late November 1980, data from the NOAA 6 AVHRR were collected for a consecutive sequence of four overpasses of the Southern California Bight. During these overpasses, a large area of ocean, including the Southern California Bight, was free of clouds. Concurrently, the NOAA vessel *David Starr Jordan* was conducting a pattern of oceanographic measurements within the field of view of the NOAA 6 satellite.

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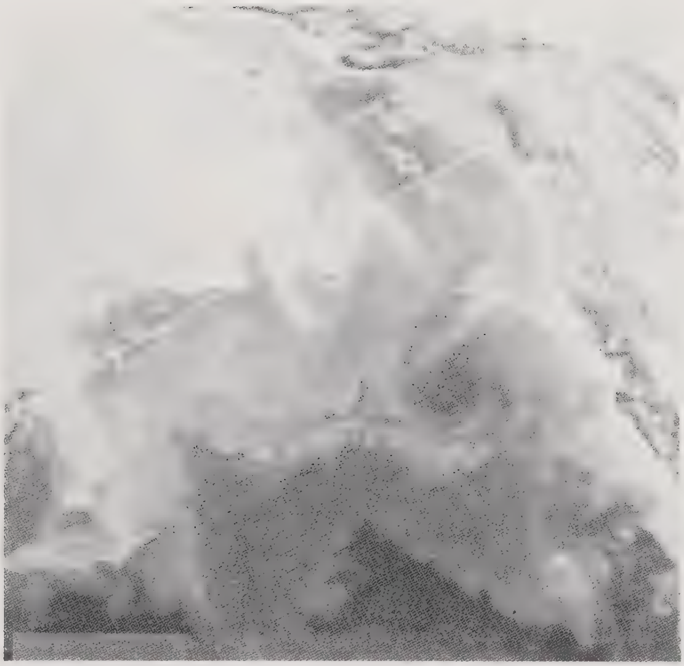

Fig. 1. Thermal image of the California Bight region made with the NOAA 6 AVHRR on November 27, 1980, at 1915 PST. Lighter shades represent lower temperatures. Different shading scales were used for land and water areas. White lines show CalCOFI transect line 86.7 (the most northern) and 90.0 sampled by R/V *Jordan* during the study. Numbered x's mark the ship's position during the sequence of satellite overpasses (discussed in text).

The clearing, which extended from inland regions to beyond 400 km offshore, was the result of a weather pattern locally termed a "Santa Ana," in which there was a broad seaward flow of low-humidity air from inland desert regions that displaced the marine cloud deck.

In this paper, multichannel atmospheric correction equations for the NOAA 6, proposed by *Bernstein* [1982] and by *McClain* [1981], are evaluated by using the satellite and in situ data set noted above. An estimate of the temporal and spatial variation of SST over small scales is made from these data, and the effect of this variation in matching satellite and in situ data sets is discussed. Additionally, changes in the temperature fields between images are examined for diurnal variation and for surface advection of horizontal temperature gradients.

Ocean Measurements

From late November through mid-December 1980 the NOAA vessel *David Starr Jordan* conducted a larval fish and oceanographic sampling survey as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program for the Southwest Fisheries Center/National Marine Fisheries Service. At the time of the satellite overpasses the *Jordan* was occupying stations along two transects identified as lines 86.7 and 90 on the CalCOFI station grid. (The CalCOFI station grid is given in numerous publications: a recent one is CalCOFI Atlas 30 [*Lynn, et al.*, 1982], which summarizes physical oceanographic distributions.) Conductivity/temperature/depth (CTD) casts were made at stations approximately every 40 miles along line 90 by using a Plessey model 9040 CTD. The ship's tracks for these two lines and the ship positions during three of the overpasses are overplotted on the IR image for the second overpass in the series (Figure 1). (The ship position for the remaining overpass fell outside the left frame of Figure 1.) Identifying landmarks, station positions, and a geographic grid are provided in Figure 2. An Ocean Data Equipment Corporation thermosalinograph recorded surface temperature continuously. The temperature probe for the thermosalinograph is located at the intake of the sea chest, about 2 m below mean water line. The temperature channel was calibrated against high-quality reversing thermometers. The CTD casts were standardized by reversing thermometers and discrete salinity samples drawn at 1 m and at 500 m, the greatest cast depth. These casts are started with the unit submerged

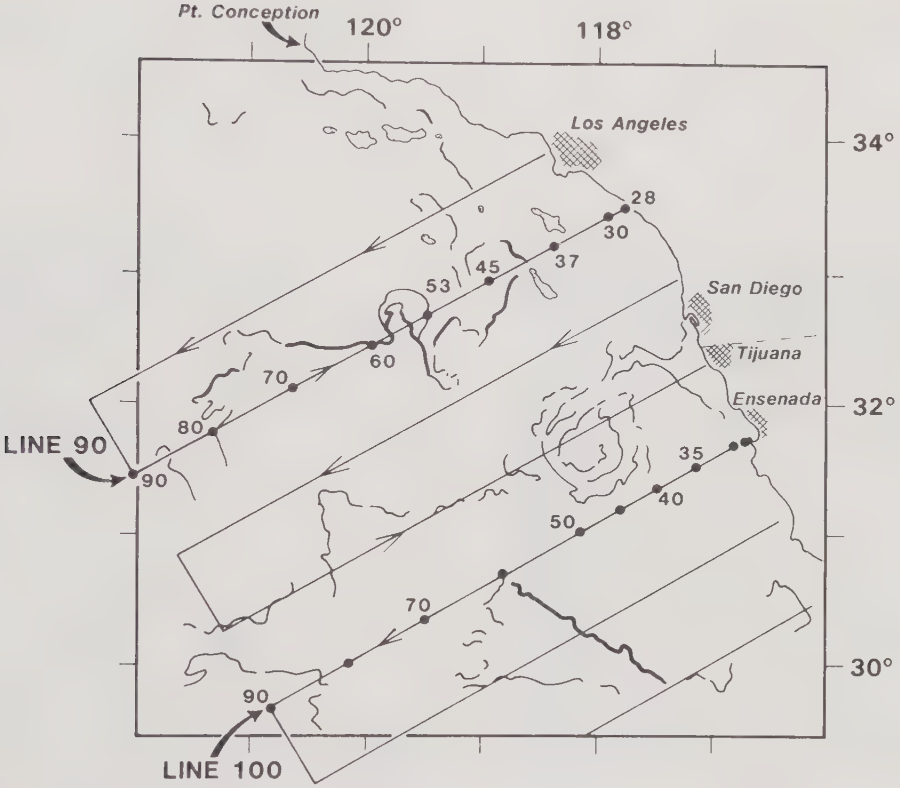

Fig 2. Schematic of thermal patterns in Figure 1 with geographic identifications, cruise track (indicating continuous thermosalinograph recording), and CTD station positions.

and hence record temperature no shallower than 1 m. Winds and weather were recorded at CTD stations.

Satellite Measurements

The AVHRR data were collected and processed at the Scripps Satellite Oceanography Facility by using the Interactive Digital Image Manipulation System (IDIMS). The raw AVHRR signal was digitized to 10-bit resolution in equal increments of energy. Then, a radiometric calibration routine based on that of *Lauritson et al.* [1979] was used to convert the channel 3 and channel 4 energy values to units of temperature. Channel 1 and channel 2 signals were converted to percent albedo by using prelaunch constants. An orbit time correction was computed and the images were registered to an earth location accuracy of 1 pixel (1.1 x 1.1 km along subtrack) by using the method of *Young* [1981]. Image registration was checked against the location of Santa Barbara Island (33°29'N, 119°02'W). The area of this island does not greatly exceed 1 km^2; hence it falls almost entirely within 1 pixel.

The first overpass was collected at 0730 PST November 27, 1980 (Julian day 332). The following three overpasses were collected at successive 12-hour intervals. These are referred to as Op 1 through Op 4, respectively; Op 1 and Op 3 are morning (descending) orbits, while Op 2 and Op 4 are evening (ascending) orbits. The subtracks of Op 1 and Op 2 fell within the bight; the subtracks of Op 3 and Op 4 fell less than 500 km to the east of it.

Description of the Study Area

Working files of full-resolution images (512 x 512 pixels) were created for analysis. Figure 1 is an image of the study area made by assigning a gray scale to channel 4 brightness temperatures of overpass 2. The image encompasses a region off southern California and northern Baja California. Point Conception is found at the upper edge of the figure and Cape Colnett, Baja California, on the lower right edge. (*Koblinsky, et al.* [1984] also used the data from these satellite passes in the study of an anticyclonic eddy and thermal fronts that lie to the north and west of the area we have framed.) Cool waters are light and warm waters are dark. The California Current transports cool waters of northerly origin southward. Inshore of the California Current, the California Countercurrent transports warmer waters of southerly origin northward (during fall and early winter). At this time the countercurrent extended northward around Point Conception as indicated by the warm (dark) coastal waters. The thermal front in the upper center of Figure 1 most probably was enhanced by the injection of cold upwelled waters into the California Current from coastal regions along central California [see *Koblinsky, et al.*, 1984]. At the thermal front the largest temperature gradient measured by the thermosalinograph is 1.7°C in 4 km. Temperatures on the cool side of the front are about 14.8°C and on the warm side 16.7°C. The warmest areas within the figure (bottom of image) are

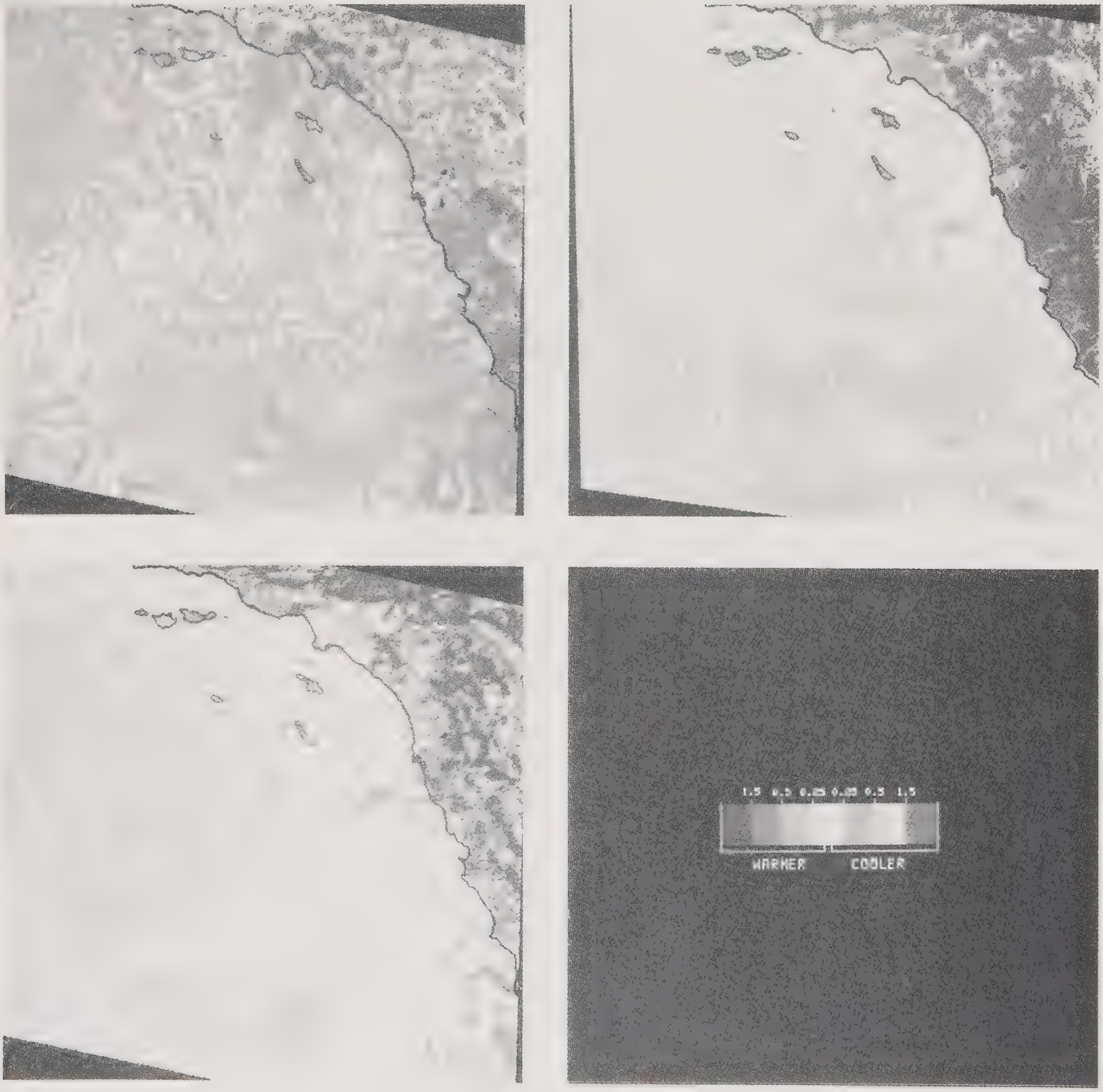

Plate 1. Differences between AVHRR channel 4 images mapped to show temperature changes during each time interval: (*a*) the difference between overpass 1 and 2; (*b*) the difference between overpasses 2 and 3; (*c*) the difference between overpasses 1 and 3; (*d*) the color key for $a-c$.

about 18°C. There is a cyclonic eddy west of Ensenada, Baja California, the center of which is warmer (at the surface) than the surrounding waters. The sense of eddy rotation was confirmed by surface thermal structure movement in the series of images and by geostrophic velocities calculated for stations on line 100 (Figure 2). Although the dynamics of a cyclonic eddy dictate a cool core, and the same relative pattern is expected at the surface,this eddy appears to be entraining even cooler surface waters, which have upwelled along the coast near San Diego, into its periphery.

These characteristics and features in the image of Figure 1 do not deviate appreciably from seasonal means or earlier observations. The characteristics demonstrating seasonal normality include surface temperature patterns and small pockets of coastal upwelling [*CalCOFI*, 1963; *Lynn*, 1967], flow patterns [*Wyllie*, 1966], and thermal fronts [*Bernstein et al.*, 1977]. Also, Reid et al. [1963] studied a cyclonic eddy in November 1959 very close to the same location as the one found in Figure 1.

THE SANTA ANA AND SUBPIXEL CLOUD DETECTION

The "Santa Ana" weather condition is characterized by winds from the midland high-desert regions, high temperatures, extremely low humidity, and complete clearing of clouds [*Sommers*, 1978, 1981]. A Santa Ana occurs when the eastern North Pacific high-pressure cell moves inland, often over northern or central California, and the inland desert low-pressure cell is situated south of it. The resulting gradient winds are directed seaward. These winds are fed by upper level dry air that descends, adiabatically warms in the eastern sector of the high-pressure cell, and is reinforced by warm dry desert air. An observer in the coastal region would note the intense blue of the sky. A Santa Ana is an infrequent occurrence in its fully developed state. It is more likely to occur in late fall and winter than at other times and typically lasts for several days. The extreme dryness associated with Santa Anas often creates serious fire hazard conditions in coastal brush and forest regions [*Sommers*, 1981]. Such conditions occurred during this study.

An important criterion for successful employment of any atmospheric correction is that the area of interest be free of clouds, including very small or transparent clouds that may remain undetected upon visual inspection of the image. The reflectance value for each pixel, as measured by channel 2, can be used to detect unresolved subpixel-sized clouds in daytime images [*Bernstein*, 1982]. A totally cloud-free atmosphere will result in an albedo of the ocean surface of less than 2% [*Bernstein*, 1982]. In our study area, no pixel showed greater than 1.7% albedo, with most pixels registering less than 1.3%. The largest albedo values were associated with a seaward projecting smoke plume originating from several brush fires. This phenomenon is discussed in a later section.

The difference between channel 3 and channel 4 and its spatial variation are also indicators of the degree of cloud contamination. This difference is used for nighttime passes when albedo measurements are not possible. The difference is usually slightly positive because of the unequal response of the two channels to water vapor. Over very humid tropical atmospheres, it can range up to 4°C or 5°C. A much larger positive difference indicates the presence of transmissive clouds or small subresolution cloud elements, whereas a large negative difference, $<$-0.9°C, is indicative of thick nontransmissive clouds [*McClain et al.*, 1983]. Although this difference, theoretically, should be very close to 0 for a dry, cloudless atmosphere, the actual differences will be slightly negative (-0.1° to -0.7°C) due to molecular absorption of atmospheric gases other than water vapor (E. P. McClain, personal communication, 1983). Within our study area, the channel difference consistently ranged between 0.0°C and -0.6°C for all four passes. Thus both albedo values for the daytime passes and the differences between channels 3 and 4 for daytime and nighttime passes confirm the relatively dry, cloud-free conditions during our experiment. In OP 4, clouds had moved into the southwest corner of the field. Our analysis is confined to the clear areas.

SATELLITE DATA NOISE REDUCTION

From its initial operation after launch, July 1979, the channel 3 signal of the AVHRR aboard NOAA 6 has been sensitive to interferences purportedly generated by improper isolation from other circuits in the spacecraft. (Channel 3 in NOAA 7 and NOAA 8 also have had the same problem. An on-gassing procedure resulted in a 90% reduction in noise level as of June 15, 1983 (NOAA 6), September 8, 1983 (NOAA 8), and September 17, 1983 (NOAA 7) (E. P. McClain, personal communication, 1983).) The interference is manifested as a noise added to the sensor signal. The noise progressively increased in magnitude with time so as to make channel 3 unusable, for all practical purposes, by May 1981. In November 1980 the noise was on the order of ±0.3°C, with occasional spikes to ±1°C (the effect of which is increased by 50%, using either SST correction equation). In imagery, most of this noise appears as a mottled herringbone pattern. However, all the major ocean thermal gradient features are easily discernible. The noise is susceptible to filtering because of its regularity.

The temperature signals sensed by channels 3 and 4 differ slightly because each responds differently to atmospheric gases and water vapor. Prior to filtering channel 3, the noise is enhanced in relation to the signal by creating a file of the difference between channels 3 and 4. This step removes most of the signal (i.e., the ocean temperature structure) and leaves the difference in response of the two sensors to atmospherics and the noise. Then, a two-dimensional Fast Fourier Transform (FFT) routine, available in IDIMS, is applied. The division between the remaining signal and the noise is subjectively identified on a display of the magnitude of the transform. The portions of the transform that contain the signal information are masked and an Inverse Fast Fourier Transform (IFT) is applied to the remainder (the noise), which then is subtracted from channel 3 to create a virtually noise-free channel 3 signal. The resulting image is very clean and shows the same fine-scale thermal structure as an image of channel 4. Plots of brightness temperature for channel 3, before and after filtering, and for channel 4 are given in Figure 3 for a line of pixels coincident with the ship's track along CalCOFI line 90. Along most of this line, the filtering appreciably reduces the noise. A problem is created, however, by the filtering procedure in the daytime images within 50 km of the coast (on the right side of the plots of Figure 3, covered by shading), where the temperatures of the filtered channel 3 deviate sharply from the unfiltered data and from the form of the channel 4 plot. This is the effect of the FFT-induced smoothing across the abrupt temperature change between ocean and land. There is also a very small shadow effect, which ripples out from the coast. It is seen as ghostly repetitions of the coastline in an image formed by differencing channels 3 (filtered) and 4, and it has an amplitude of approximately 0.1°C. The problem was not evident in the night images, when the ocean/land temperature differences were small. In this study we have avoided the heavily affected areas within 50 km of the coast; the small-amplitude ripple effect was ignored. A technique that may avoid this problem, but which we have not tested, is to assign to all land areas a single value of temperature difference close to that found in coastal waters prior to applying the FFT filter.

CORRECTED SATELLITE AND IN SITU SST

The dual-channel empirical equation for calculating surface temperature (T_{sfc}) from NOAA 6 data given by *McClain* [1981] is

$$T_{sfc}=1.5T_3-0.44T_4+1.12$$

where T_3 and T_4 are brightness temperatures for channels 3 and 4 and all temperatures are in degrees Celsius. It was developed from a simulation model by using measured atmospheric moisture and temperature profiles, and it was adjusted by linear regression to fit a set of 41 paired observations of ocean and satellite data selected for seasonal and geographic diversity. *Bernstein* [1982] developed an alternate version of a temperature correction equation by using only daytime passes, a rigorous screening process to obtain cloud-free satellite data, and a different set of paired ocean and satellite data. His version, after transformation and using temperatures in degrees Celsius, is

$$T_{sfc}=1.3826T_3-0.31T_4+1.72$$

The Bernstein version gives slightly higher temperatures: 0.3°C higher for $T_3 = 15°C$ and $T_3 - T_4 = 4°C$ (moist atmosphere) and 0.9°C higher for $T_3 = 15°C$ and $T_3 - T_4 = -0.5°C$ (dry atmosphere). The offset increases slightly for higher temperatures.

One of the critical steps in the algorithms of *Bernstein* [1982] for NOAA 6 and *McClain et al.* [1983] for NOAA 7 is the selection of those elements of a satellite image that are most likely to be free of contamination by clouds. Criteria for selection include the magnitude of the readings from various channels (to fall within specified ranges), the relationship between the readings of various channels, and the degree of variation among neighboring data elements. It is characteristic of these selection processes to greatly reduce the spatial resolution. Generally, these algorithms are used to produce large-scale SST maps based on an accumulation of multiple satellite passes. Because we are examining a single area that we judge to be uniformly clear of cloud contamination, we have applied the SST correction formula to full spatial resolution of the AVHRR data without the element-by-element selection.

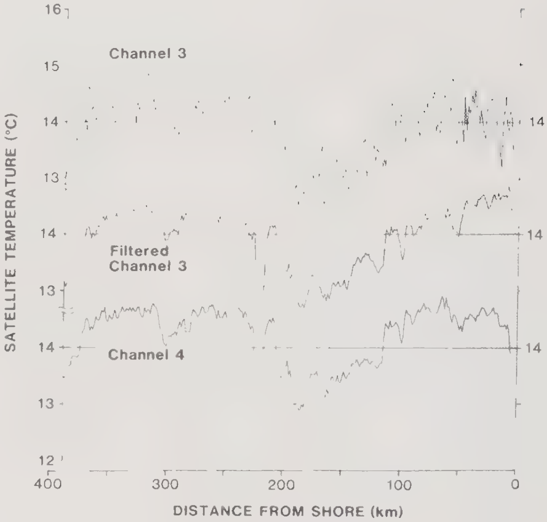

Fig. 3. NOAA 6 AVHRR temperature profiles along CalCOFI line 90 from overpass 3 (morning): top, unfiltered channel 3; middle, channel 3 after application of FFT filter; bottom, unfiltered channel 4. Lightly stippled area shows extent of land/water boundary effect in the filtered image.

Estimates of sea surface temperature were computed by using both the Bernstein and McClain atmospheric correction equations. In both instances the input was channel 4 and filtered channel 3 brightness temperatures. Both versions of SST, computed for OP 3, are plotted in Figure 4 for the line of pixels corresponding to CalCOFI line 90. The thermograph trace, reconstructed to a linear distance scale, is plotted with both versions of satellite SST. This segment of the thermograph trace was recorded over 36 hours on an inbound leg of the survey pattern. The passage times of OP 3 and OP 4 are marked on the time abscissa for the thermograph.

There is excellent agreement in the spatial structure of SST between the satellite and ship records. The agreement is best where the records are more nearly coincident in time (in the neighborhood of the time of OP 3). In terms of values of temperature for this daytime overpass the Bernstein equation has a mean bias of +0.5°C in relation to the in situ measurements and the McClain equation a bias of -0.4°C. In both cases they are within the range of scatter claimed by the authors; however, they differ from each other by 0.9°C, more than their individual anticipated range of scatter. The biases attained by these simple linear models, however, are a considerable improvement over earlier versions. There is a variety of possible causes for the level of uncertainty in the models, and these causes may also be responsible for the differences between them. Both models were fitted to sets of

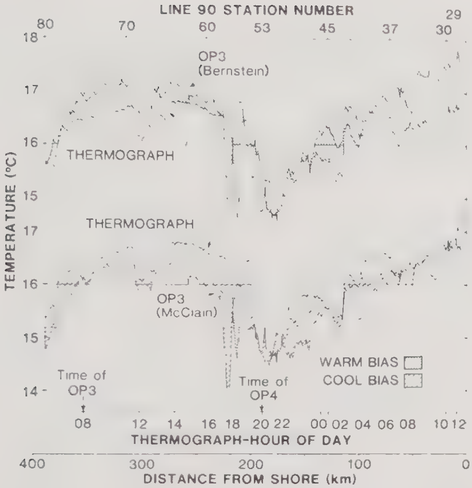

Fig. 4. Line 90 *Jordan* thermograph profile and corresponding satellite profiles using data from November 28 morning overpass (Op 3). Channel 4 and filtered channel 3 were used for Bernstein's (upper) and McClain's (lower) atmospheric correction formulae. Lightly stippled area same as Figure 3.

ocean temperature measurements (selected for quality) and corresponding satellite-derived measurements (selected as cloud-free). These paired data were collected for all seasons and for low to high latitudes. By necessity, there are tolerances in time and space needed to match ocean data to corresponding satellite data. *Bernstein* [1982] permits several tens of kilometers and several days; *McClain et al.* [1983] permits 25 km and 1 day. These tolerances contribute to the variance in deriving a satellite/ocean SST relationship. Additional problems in pairing remotely measured and in situ temperatures, noted by the authors, include using satellite areal averages versus ocean point values, diurnal variations, and true surface or "skin" values versus bulk values (usually measured at 1 or more meters below the surface). All but the last problem can be examined in our series of images.

Small-Scale Spatial and Temporal Variations

Plots of channel 4 brightness temperatures along line 90 for Op 1 and Op 3 are plotted on a common scale in Figure 5. These transects cross a meandering thermal front three times, producing the large gradients in the center of the figure. The gradients are about 2°C in 10 km. Elsewhere in this transect there are gradients of 0.6 to 0.8°C in several tens of kilometers. The offset of one trace from the other shows the changes in 24 hours. A lateral translation (i.e., advection) of some of the gradient features has produced local temperature changes equal in value to the spatial temperature differences. The large gradient features in the center of the transect moved eastward 15 km in this period, and the gradient near 100 km from shore moved westward 20 km. The 0.8°C cooling that occurred at 300 km from shore was caused by advection transverse to this line (determined by inspection of the sequence of thermal images). The offshore two thirds of the transect shows an overall cooling on the order of 0.3°C. These temperature differences over short distances and periods will quickly degrade a matchup of satellite and in situ measurements that are not taken within a few hours and a few kilometers of each other. Such a requirement, however, is apparently too stringent to permit a sufficient set of data pairs for establishing a regressional relationship that has reasonable geographic and seasonal applicability. Thus the necessry temporal and spatial tolerances in associating ocean and satellite measurements can account for a part of the variance in the derived temperature relationship.

Ocean Skin Temperature

Radiometers measure the "skin" or surface temperature of the ocean, which is usually a few tenths of a degree Celsius cooler than the temperature some tens of centimeters below [*Paulson and Simpson*, 1981, and other references therein]. This temperature difference occurs because the vertical heat flux just below the surface is usually upward. Most of the temperature difference occurs in the upper few millimeters, where molecular processes dominate. Below this thin layer, turbulent mixing dominates and the temperature gradient is negligible [*Simpson and Paulson*, 1980]. The *Bernstein* [1982] and *McClain* [1981] models for correcting satellite IR brightness temperatures were empirically fitted to bulk temperatures (1 m and deeper); hence they compensate, in a rough sense, for the bias caused by the cool skin. The magnitude of the temperature difference in the upper 10 cm, however, is dependent upon wind speed and heat transfer rates. *Paulson and Simpson* [1981] find that only half the variability in the radiometric SST is accounted for by the variability in the subsurface (1 m) temperature. Based upon their experiments, the unaccountable variability is at least 0.1°C to 0.3°C. Moreover, under very low wind conditions and strong (summer) solar heating, it can be as high as 0.5° to 0.6°C. *Hasse* [1971] showed that the diurnal temperature variation within this skin layer is somewhat greater than within the rest of the diurnal layer, approximating in phase and range the overlying air temperature.

Diurnal Effects

The collection of sequential imagery from day and night NOAA 6 overpasses during this study and the high

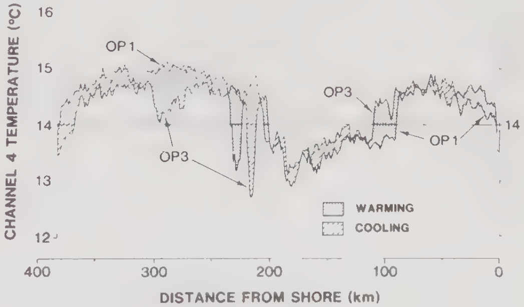

Fig. 5. AVHRR channel 4 temperatures along CalCOFI line 90 from overpasses 1 and 3 (24-hour interval).

accuracy of geographical registration of the data allowed us to examine the effects of diurnal heating as detected by the AVHRR. The formation of a shallow (less than 20 m deep) diurnal surface layer under conditions of light winds and strong insolation has been observed by numerous investigators [see, for example, *Jacobs*, 1978; *Kaiser*, 1978] and numerically simulated by *Dickey and Simpson* [1983]. During the day irradiative heating increases the heat content of this layer, the highest temperatures occurring in the late afternoon. The surface layer then begins to gradually lose heat during the night (or mixes the heat downward) until the temperature of the diurnal layer matches the temperature of the underlying water. A mixed layer condition persists until irradiative heating once again becomes appreciable, which is around 1000 local time for midlatitudes in autumn.

During late November, in the Southern California Bight, sunrise is at approximately 0700 and sunset at 1700 PST. The morning orbits of NOAA 6 cross the study area during the period when the diurnal layer is absent. The evening orbits pass over 3 to 4 hours after the expected peak development of a diurnal layer. The surface temperatures along line 90 are given in paired line plots by using channel 4 temperatures for each of three day/night 12-hour intervals in Figure 6. Diurnal variation in brightness temperature is clearly evident. The evening (1930 hours) temperatures are seen to be higher than the morning (0730 hours) ones by 0.2 to 0.9°C, except for small areas where shifting thermal gradients counteracted or reinforced the diurnal cycle. These differences are larger and more prevalent than the 24-hour differences of Figure 5. The differences between channels 3 and 4 remain substantially constant from OP 1 to OP 4, suggesting that the atmospheric conditions also remained constant. Therefore, the overpass-to-overpass differences in channel 4 brightness temperatures are equivalent to the differences in calculated sea surface temperatures and were chosen for examination because they are the most noise-free. These 12-hourly differences in channel 4 brightness temperatures measure diurnal heating and cooling of the oceanic thermal molecular boundary layer (the skin effect), which in turn reflects the diurnal heating and cooling of a shallow surface layer below it. The times of passage of NOAA 6 may not have caught the extremes in surface temperature, but it is not likely to have missed by much.

Maps depicting the surface temperature changes were created by subtracting thermal images, pixel by pixel, and assigning a uniform color scale to the resulting difference (Plate 1). The first of these difference maps (Plate 1*a*) reveals the overall diurnal warming, shown by yellow and red tones, during the period between OP 1 and OP 2 (morning to evening). The greater part of the image has a temperature increase in the range of 0.25°C to 0.5°C. Warming in excess of 0.5°C occurs south and west of Point Conception, southwest of greater Los Angeles, off Baja California, and more generally within 150 to 180 km of the coast. (Not evident in this choice of color scale is that ocean warming in excess of 1°C is confined to high gradient regions, where advection played a dominant role.) A temperature change between -0.25°C and +0.25°C occurs in the warm offshore waters (middle of Plate 1*a* and to the left), especially south of the leading edge of cold water entering from the northnorthwest. There is an overall diurnal cooling in the subsequent period between OP 2 and OP 3 (evening to following morning), shown by green and blue tones (Plate 1*b*). The picture of cooling is roughly the reverse of the picture of warming, however, in some regions the range of diurnal cooling exceeds the warming. Most of the image has a temperature change in the range of -0.5°C to -1.5°C. (Actually the only cooling in excess of -1.0°C occurs south and west of Point Conception.) The movement of thermal gradient features over these periods produced juxtaposed patterns of strong warming and cooling in both images that mimic the features and indicate their direction of movement. For example, the cold plume extending seaward from the coast near Tijuana (Figures 1 and 2) appears in Plate 1 (especially Plate 1*c*) as paired warm and cold features because the plume shifted northward in the interval. The 12-hour temperature differences between OP 3 and OP 4 (not shown) are similar in pattern to Plate 1*a*, except that the warming was greater by nearly 0.3°C in the central and coastal portion of the image; the western and southwestern portions were contaminated by the return of offshore clouds and moisture in OP 4.

The sequence of 12-hourly SST differences shows a larger range in those waters in which the penetration of diurnal heating is constrained to a shallow layer. This includes turbid coastal areas, where the depth of penetration of solar irradiation is restricted by enhanced absorption caused by biological productivity. As a result these areas frequently have a shallow thermocline, which restricts the depth of vertical mixing. The area off Los Angeles is an example of such biologically productive waters (Plates 1*a* and 1*b*). Such observed differences in the diurnal ranges, based on variation in optical characteristics and mixed layer depth, are consistent with the results of numerical simulations by *Simpson and Dickey* [1981] and *Dickey and Simpson* [1983]. A larger range also occurs in the large plume of cool water extending southward and southeastward from near-shore regions off central California and reaching offshore of the southern Channel Islands in which infusion of coastal upwelled waters produces considerable enrichment of phytoplankton [*Simpson*, 1984]. An example of regional contrast of diurnal SST range on a much smaller scale is found in the false color images 220 km southwest of Ensenada, Baja California, where a 1°C thermal front separates a wedge of warm water to the south from cooler waters to the north (Figures 1 and 2). The warmer waters experience a wider range of diurnal change, >0.5°C, than the cooler waters, <0.5°C (Plates 1*a* and 1*b*). These observations suggest that two very different regimes of heat flux and vertical mixing might have operated on opposite sides of the front. These examples offer an interesting extension of the applicability of satellite radiometric data, and they warrant further study.

Over the encompassing 24-hour period between OP 1 and OP 3, (Plate 1), the differences are generally smaller, except for the areas affected by the movement of gradient features, most of which show larger changes. In the far offshore areas and the cooler northern waters, cooling predominates, some of which is in excess of -0.5°C. Negligible differences predominate in the central

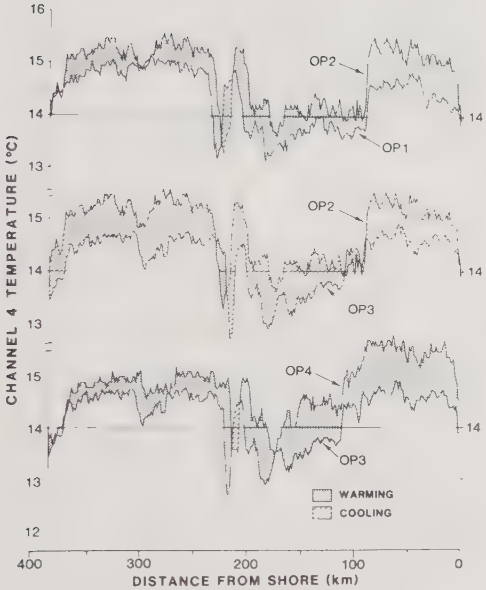

Fig. 6. AVHRR channel 4 temperature profiles along line 90, showing 12-hour differences. Shading shows extent of warming or cooling during the time interval: upper, overpass 1 (0730 hours) and overpass 2 (1930 hours); middle, overpass 2 (1930 hours) and overpass 3 (0730 hours); lower, overpass 3 (0730 hours) and overpass 4 (1930 hours).

coastal region. Moreover, the waters off Baja California, which may be remanent of earlier upwelling, show a overall small rise in temperature. The image of 24-hour temperature differences between Op 2 and Op 4 (also not shown) exhibits small temperature increases in nearshore areas, while offshore areas have negligible changes or minor cooling.

The *Jordan* CTD casts provide some small evidence of a diurnal layer. Of the 15 temperature/depth profiles, each from a different location, three were made in the late afternoon or early evening, when a warm diurnal layer would be expected to exist. Of these three, two casts show evidence of a diurnal layer. The cast at station 90.53, made at 1945 hours, shows, an 11-m-thick surface layer that is 0.2°C warmer than the remaining body of the surface layer, and the cast at station 90.60, made at 1525 hours, shows a 7-m top layer that is 0.2°C warmer. The third afternoon cast, station 100.70, had no diurnal layer but was not taken until a week after this Santa Ana clearing. The CTD casts provide only marginal confirmation for the development of a diurnal layer because their scattered deployment was not entirely satisfactory for this purpose. However, at the positions of the two stations the temperature differences between Op 3 and Op 4 (from Figure 6) are in the range of 0.4 to 0.5°C. The CTD casts show only half as much diurnal variation as the satellite brightness temperatures.

Discussion

The local balance of heat exchange through the sea surface can be expressed as $Q_T = Q_I + Q_L + Q_A$, where Q_I is the incident solar irradiation input corrected for clouds and albedo, Q_L is the combined loss resulting from net back radiation and latent and sensible heat exchange, Q_A is the heat exchange caused by advection, and Q_T is the balance of the preceding terms. For a clear day at this latitude and time of year the solar irradiation (corrected for 7% albedo) is 292 cal cm^{-2} d^{-1}, as calculated by *Lumb* [1964], or alternately 326 cal cm^{-2} d^{-1}, as taken from tables adapted from Berliand by *Johnson et al.* [1965]. Psychometric measurements taken aboard the *Jordan* formed the basis for calculations of heat loss terms. Winds, barometric pressure, air temperature, wet bulb temperature, and a bucket temperature were recorded at nine stations during the period of the Santa Ana conditions (Table 1). The measurements were taken as a matter of routine, and no precautions were taken to ensure their quality. Despite this caveat, they are adequate for estimating the surface heat budget terms. The combined heat losses were calculated for each set of measurements of the nine stations (Table 1) after the methods given in *Clark et al.* [1974]. The balance of the gain and loss terms is on the order of +100 cal cm^{-2} d^{-1}. Long-term (1961-1971) mean values of Q_I and Q_L interpolated from Clark et al. for this region and time of year are 238 and 272 cal cm^{-2} d^{-1}, respectively. Our observations show a greater gain and lesser loss, but these differences are well within the range of scatter for these terms.

A notable result of the psychometric computations is that the relative humidity for these stations ranged from 70% to 91%, increasing with time (Table 1). Values ranging from 10% to 28% were reported for Los Angeles (*The Los Angeles Times*) and 15% to 69% for San Diego for these same days (*The San Diego Union*). The values of relative humidity calculated from the ship measurements are in apparent contradiction to the description of a dry atmosphere. It is characteristic of a Santa Ana condition, however, that following the displacement of the clouds and the cool moist marine layer by warm dry easterly winds there is immediate renewed evaporation into a thin layer of air near the surface. The evaporation cools the air and forms a stable layer in which water vapor saturation is approached [*Liepper*, 1948; *Noonkester*, 1979]. Such a shallow layer of cool moist air below the warm dry air of Santa Ana winds was also observed by *Sommers* [1978]. Satellite radiometers integrate the effect of atmospheric water vapor throughout the path length of observation. We have already noted that the magnitude and sign of the difference between IR brightness temperature of channels 3 and 4 describe a dry atmosphere over the ocean for the same days. An additional characteristic of IR brightness temperatures is that the thermal contrast between warm and cold water is suppressed by the water vapor content of the atmosphere; in a dry atmosphere there is no apparent loss of gradients in the data field [*Huh et al.*, 1982]. A comparison of either channel 3 or 4 brightness temperatures (Figure 3) with the thermograph data (Figure 4) shows no suppression of measured gradients, supporting the case for a dry atmosphere. Consequently, these observations show that the marine layer was very shallow indeed; the psychometric measurements were made at a height of 4 m above the sea surface.

The heat input occurs over a period of about 9

TABLE 1. Psychometric measurements and observations of mixed layer depth aboard the NOAA vessel *David Starr Jordan* for the period inclusive of the four satellite passes identified in the text as OP 1 through OP 4. Calculations of the combined heat loss term (Q_L) from the heat exchange balance (see text) and relative humidity appear in the right-hand columns.

								Air Temp., °C					
Date, 1980	Time, PST	Station	Lat., N	Lon., W	Wind Speed m s^{-1}	Wind Direction, °T	Pressure mbar	Dry	Wet	Bucket Temp., °C	Mixed Layer Depth m*	Q_L, cal cm^{-2} d^{-1}	Relative Humidity, %
Nov. 27	0100	87.60	32°60'	120°21'	6	340	1024	16.1	13.0	14.9		237	70
Nov. 27	0557	87.70	32°39'	121°02'	7	340	1024	16.1	14.0	14.7		246	79
Nov. 27	1130	87.80	32°19'	121°43'	8	340	1025	17.8	15.8	15.7		275	81
Nov. 27	1636	87.90	31°59'	122°24'	7	0	1023.5	15.8	14.2	15.8		190	84
Nov. 27	2150	90.90	31°25'	121°59'	9	340	1023.3	16.6	15.2	17.2	23	168	86
Nov. 28	0400	90.80	31°45'	121°19'	7	330	1019.9	15.8	14.0	15.6	15†	202	82
Nov. 28	0950	90.70	32°05'	120°38'	7	340	1020	17.1	15.3	16.8	50	201	83
Nov. 28	1525	90.60	32°25'	119°58'	6	330	1017	18.0	16.7	16.7	35	203	88
Nov. 28	1935	90.53	32°39'	119°29'	5	340	1017	15.3	14.4	14.8	35	179	91

* Depth where temp is 0.2°C < SST exclusive of diurnal layer.

† This value is probably unrepresentative of the region.

hours. If the rate of loss may be considered constant over 24 hours and advective exchanges are ignored, then 230 cal cm^{-2} are stored during daylight hours and 130 cal cm^{-2} are lost at night. Assuming the diurnal heat gain is restricted to 7 to 11 m, as is true of the CTD casts, the diurnal increase of temperature would be on the order of +0.25°C (actually the diurnal temperature cycle is more complex, but this simple approach serves our purpose). This estimate is consistent with the CTD casts and is consistent with the diurnal modeling studies [*Dickey and Simpson*, 1983] for a wind speed near 7 m s^{-1}, but it is less than the observed differences of brightness temperatures. The excess heat gain of 100 cal cm^{-2} over 24 hours is stirred throughout the surface mixed layer (Table 1), resulting in a day-to-day temperature increase of 0.04°C or less. This increase is negligible. The observed IR brightness temperature differences over 24 hours (Figure 5 and Plate 1*c*) suggest that local advection may have played a more important role than the balance of the other heat exchange terms during this study. The equatorward flowing California Current in the offshore waters and the poleward flowing California Countercurrent nearshore [*Wyllie*, 1966; *Lynn et al.*, 1982] provides the correct sense of flow to produce the offshore/nearshore pattern in the 24-hour temperature differences (Plate 1*c*). Sections of geostrophic velocity and associated temperature (Figure 7) for lines 90 and 100 (line 100 was occupied 11 days after line 90) give evidence that equatorward advection of cooler offshore waters and poleward advection (shown hatched in Figure 7) of warmer waters might account, in part, for the differences over 24 hours. It is clear, however, that the magnitude of the day/night brightness temperature difference is not satisfactorily explained by the ocean measurements. It may be that this difference is due, in part, to a variation in magnitude of the ocean skin effect. The results of this comparison point to a need for a better understanding of the heat exchange processes in areas cleared of clouds by warm continental airflow and the effect of these circumstances on the nature of satellite-based radiometer measurements.

It is also clear that diurnal differences can have an appreciable effect on satellite SST estimations and can be an appreciable cause of variability if data from both nighttime and daytime orbits are used during one study. If agreement between in situ and satellite measurements is sought, it is preferable to use satellite data from the orbit least affected by diurnal surface heating. For the west coast of the United States this would be the 0730 orbit of NOAA 6, the 0400 orbit of NOAA 7, and the 0800 orbit of NOAA 8.

Bernstein's atmospheric correction equation was derived from satellite data restricted to early morning passes. (The same restriction was not applied to the in situ measurements.) Applying his equation to the evening passes gives a bias of +1.2°C. Such an application appears to be inappropriate. *McClain's* [1981] equation was also derived from morning overpasses (E.P. McClain personal communication, 1983). As applied to the evening passes, however, his equation gives a bias of +0.4°C, nearly the same bias as Bernstein's equation gives for the morning overpasses. The thermograph recorded continuously and should show effects of diurnal warming at 2 m over the 36 hours it took to complete line 90. Therefore, the bias between a transect of corrected satellite temperature, a truly synoptic measurement, and the thermograph should vary between the periods in which the thermograph detected the penetration of diurnal warming and those in which it did not. A change of 0.2°C in the bias of satellite and thermograph between the morning of OP 3 and the following afternoon is suggested in Figure 4. However, the complexity of the ocean's surface thermal structure and its movement make it difficult to ascertain.

Smoke — Is There an Effect Upon Temperature Estimates?

Visual imagery from channel 1 data and reflective IR imagery from channel 2 reveal large plumes of smoke from coastal forest fires, extending southward and westward over the bight. The major fires occurred a short distance inland of the beginning of line 90. Beyond the immediate region of the source, the smoke produces an increase in albedo above that in the clearest areas of 0.4 to 1.0%. The smoke occurs in large sweeping patterns that have a characteristic scale much larger than the ocean thermal patterns. If the smoke produced a detectable

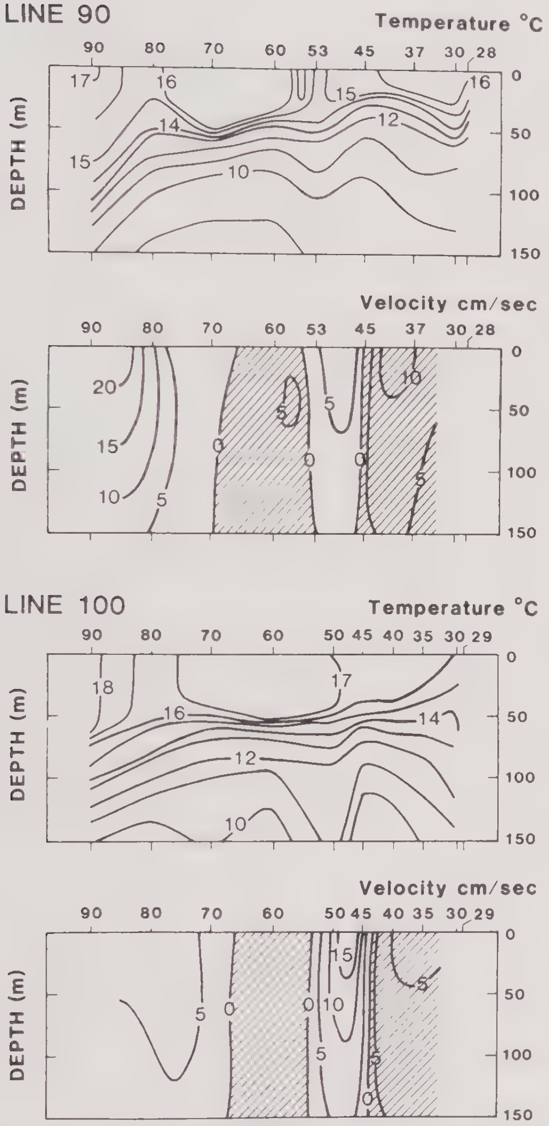

Fig. 7. Vertical sections of temperature and corresponding 0/500 db geostrophic velocity sections for lines 90 and 100. Hatching indicates poleward flow.

effect upon the IR measurements, then the smoke patterns would be found in the IR images, especially in the temperature difference between channels 3 and 4. No effect of this kind was found.

Conclusions

1. Noise in NOAA 6 channel 3 can be largely eliminated by filtering for those overpasses collected prior to spring 1981. The use of unfiltered data in estimating SST can produce spot errors as large as 1.5°C.

2. Both atmospheric correction equations tested in this case study produced estimates of SST that matched the in situ measurements within the expected range of scatter. Bernstein's equation produced a bias (for a daytime pass) of +0.5°C and McClain's gave -0.4°C. Bernstein's version, which was derived exclusively from daytime data, produced a bias slightly in excess of 1°C when applied to nighttime data because of a diurnal variation.

3. A diurnal variation in satellite brightness temperature on the order of 0.25°C to 1.0°C was recorded in a sequence of four images. In situ measurements did not register the range in diurnal variation seen in the satellite data. This disparity is not entirely understood. There are complex heat exchange processes that occur at and near the air/sea interface (1 to 2 μm deep) where temperature is sensed by satellite radiometers and other dynamical processes that occur at depths of 1 to 3 m, where in situ measurements of surface layer temperature are made.

4. When there is a diurnal warming of 0.3°C or more, intermixing of daytime and nighttime data will cause problems. The problems are avoided by restricting analysis to overpasses that occur at late night and early morning hours. Such a restriction should provide more reliable estimation of SST and a better match to in situ measurements. Effects of diurnal heating in in situ measurements should likewise be avoided, if possible.

5. Differences in time and/or space between satellite and in situ measurements can cause disagreements of up to 1°C or more because of surface thermal structure and its movement.

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